THE LOWER FUNGI

PHYCOMYCETES

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THE LOWER FUNGI

PHYCOMYCETES

BY

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PREFACE

This book is intended by the author to serve a two-fold purpose. The urgent need of the research worker in mycology and plant pathology for an adequate treatment of the taxonomy and morphology of the fungi is generally recognized. Though it is clearly impossible to provide this for the whole group within the limits of a single volume, the attempt is made here to meet the need for the Phycomycetes. No effort has been spared in the endeavor to have the taxonomic presentation thoroughly modern and complete. Keys are provided to all genera, and citations are given to much of the outstanding literature. At the same time the author has tried to present the subject matter in such a fashion that the book would serve in college and university classrooms as a text or reference work for beginning and advanced students.

In formal courses in mycology time is usually so limited that it is impossible to cover the entire field of the fungi in other than a hurried and superficial manner. Some teachers avoid this difficulty by confining the laboratory studies to one of the larger subdivisions of the group. This permits the student to concentrate his efforts and to obtain a type of intensive training which fits him to proceed on his own resources in the remainder of the field. For a course of this character no group of the fungi serves the teacher's purpose better than do the Phycomycetes. Their diversity of form makes them especially suitable from the point of view of comparative morphology, and in many genera the species lend themselves readily to cytological, biological, cultural, and taxonomic studies. It is hoped that this book will be found useful as a text in connection with laboratory courses of this type. In any case it will afford a basis for systematic collateral reading on the lower fungi and related groups of organisms.

Over a period of years it has been the author's practice to provide his classes with a mimeographed syllabus, outlining the classification of the fungi and introducing the student to the various phases of the broad field of mycology. This syllabus,

occasionally revised and amplified, has served essentially as a text, and its presentation in book form has long been contemplated. The present volume represents the outcome of that plan in so far as the lower fungi are concerned. It is, thus, the natural outgrowth of the author's experience as a teacher, and is in a large part a compilation based on the literature. No claim is made that it embodies to any noteworthy extent knowledge gained from personal research throughout the group.

In even a cursory examination of the following pages the reader will note that the treatment given the various families and genera is not uniformly detailed. Some groups demand a fuller discussion on account of their exceptional scientific interest; others have received it because of their outstanding economic importance. Though the author has allowed himself considerable latitude in this regard, the effort has been made to stress the material which contributes most to the usefulness of the book.

The plan of providing a separate bibliography at the close of each chapter has been followed from the conviction that the segregation of the references in this manner aids the student in gaining a general knowledge of the literature. It makes easier also the selection of papers for supplementary reading. The bibliographies have been carefully prepared. Every reference included serves a definite purpose, and is cited in the text. If errors in these citations are discovered the author will appreciate having them called to his attention. Though it is not possible to state with assurance that all the literature published prior to any given date has been incorporated, a determined attempt has been made to keep the manuscript up-to-date during the process of its preparation.

The omission of a glossary has been deliberate. Terms are printed in boldface type at the points in the text at which they are defined or their use definitely indicated. This explanatory matter is available through the index.

For permission to reproduce illustrations from the works of others the author is under deep obligation to a large number of individuals and institutions in this country and abroad. Though the list is so long that detailed enumeration here seems inadvisable, full credit is given in the legends accompanying the figures. A uniform spirit of courtesy and generosity has been encountered in every direction in this connection.

In conclusion the author wishes to express his gratitude for the continued support and encouragement given his efforts by his colleagues and students, and by his friends in other institutions. Without this cooperation the laborious undertaking would not have been begun and hardly could have been completed

H. M. FITZPATRICK.

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CHAPTER I

INTRODUCTION

As botanists are not yet in complete agreement with respect to the limits and interrelationships of the various groups of primitive plant life, it is necessary that the extent of the lower fungi as here understood be indicated. It is desirable also that at least brief consideration be given to the groups of organisms which lie near them in the classification.

Thallophytes.—The plant kingdom is divided by systematists into several large primary subdivisions. The lowest of these embraces all the primitive forms of plant life, and is named by most writers the **Thallophyta.** In this large and diverse assemblage the vegetative portion of the plant is usually very simple in type, and in general lacks the definite differentiation into root, stem, and leaf which characterizes higher plants. This simple vegetative plant body has been termed the **thallus**; hence the name Thallophyta meaning thallus plants. In the group as a whole the thallus is extremely simple, and in many of the lower forms consists of only a single cell. Among the higher forms it sometimes shows considerable differentiation. Moreover, in some groups of plants above the Thallophyta the vegetative body is simple and has been called the thallus. In such cases the relative simplicity of the reproductive processes serves to separate the Thallophyta from higher forms.

Although no two of the various standard classifications of lower plants agree in detail, the following brief outline of the major subdivisions of the Thallophyta represents in the main the most generally accepted arrangement, and will, in any case,

serve as a basis for discussion. Names included in parentheses are regarded here as synonyms.

Thallophyta

I. Myxothallophyta (slime thallophytes)
- *A*. Acrasieae
- *B*. Labyrinthuleae
- *C*. Myxomycetes (Mycetozoa, slime moulds)
  1. Exosporeae, *i.e.*, *Ceratiomyxa*
  2. Endosporeae (Myxogastres)

II. Euthallophyta
- *A*. Bacteria (Schizomycetes, fission fungi)
- *B*. Fungi (Eumycetes)
  1. Phycomycetes (**lower fungi**)
  2. Ascomycetes
  3. Basidiomycetes
  4. Fungi Imperfecti
- *C*. Lichens (Lichenes)
- *D*. Algae
  1. Cyanophyceae (Schizophyceae, blue-green algae, fission algae)
  2. Chlorophyceae (green algae)
  3. Phaeophyceae (brown algae)
  4. Rhodophyceae (red algae)

The green coloring matter, **chlorophyll**, which occurs in practically all higher plants, is absent in several of the groups of the Thallophyta. It is present in at least the majority of the algae, and in a restricted sense perhaps may be said to occur in the lichens. It is wholly absent in the Myxothallophyta, bacteria, and fungi.

In the presence of sunlight, plants containing chlorophyll are able to synthesize the carbohydrates necessary to their metabolism from the carbon dioxide of the air and from water. Forms of life lacking it are dependent on green plants for the elaboration of their carbohydrate food. All non-chlorophyll containing organisms (animals, slime thallophytes, bacteria, fungi) must lead, consequently, a dependent existence, either as parasites in living plants or animals, or as saprophytes in dead or disorganizing plant or animal remains.

Algae.—In their possession of chlorophyll and in their consequent ability to lead an independent existence the algae are strikingly different from the colorless thallophytes. It may be assumed that they represent the primitive type from which the higher green plants arose. In the morphology of the thallus and organs of reproduction the group exhibits great diversity.

At one extreme it is represented by unicellular microscopic forms, and at the other by species of complex structure, some of which are of great size. The members of the group are chiefly aquatic, and include the pond scums and sea weeds familiar to all students of nature.

Though chlorophyll occurs in general throughout the algae the thallus is distinctly green only in the Chlorophyceae. In the Cyanophyceae, Phaeophyceae, and Rhodophyceae other coloring matter is present in sufficient amount to obscure the green, and give the thallus another characteristic color. Older algologists used the color of the thallus as a basis for the primary separation of the group, and recognized as major subdivisions, blue-green algae, green algae, brown algae, and red algae. Though these groups are still recognized as constituting in a broad way a convenient separation, there is a pronounced tendency in modern classification toward basing separations wholly on morphology (*e.g.*, West and Fritsch 1927). Where color fails to coincide completely with morphology rearrangement has occurred. It is to be expected that future research will result in even more extensive revision and the disappearance of the old absolute separation based on color.

In some of the more recent treatments, the blue-green algae (Cyanophyceae) are removed from the algae, are renamed the Schizophyceae, and together with the Schizomycetes (bacteria) are made to comprise a lower primary subdivision of the Thallophyta termed the Schizophyta. The group thus constituted is regarded as occupying an isolated position in the phylogenetic arrangement, and its members are believed to be very primitive. Both in the bacteria (fission fungi) and blue-green algae (fission algae) reproduction is accomplished almost exclusively by means of simple vegetative cell cleavage or fission. Though spores of a simple type occur in both groups, complicated reproductive structures and processes, comparable to those of other thallophytes, are lacking. The nucleus, if not actually absent, is at least far less definitely organized than in other plants.

The blue-green color of the Cyanophyceae is believed to be due to the presence in the protoplasm of two associated pigments, one blue, the other green. The blue coloring matter has been named **phycocyanin.** That the green is chlorophyll seems not entirely certain. It does not occur in distinct chloroplasts, and may be in chemical combination with the blue pigment.

include them in the **Protozoa.** In some modern classifications no attempt is made to maintain a definite line of separation between the plant and animal kingdoms at their lower levels. Instead the group **Protista** is used to include the primitive forms of life which lie on the borderline. This is indicative of the general state of uncertainty concerning the interrelationships of these various simple forms, but should not be assumed to have resulted from ignorance of the various individual groups.

Myxomycetes.—Knowledge of the taxonomy of the Myxomycetes (Mycetozoa, slime moulds) has reached a high plane, the group having been long known and critically studied. The monographic treatises of Lister (1925) and Macbride (1922) are excellent and comprehensive. Moreover, investigations by Jahn (1907, 1908, 1911), Harper (1900, 1914), Harper and Dodge (1914), Strasburger (1884), Bisby (1914), Olive (1907), Skupiénski (1918, 1927, 1928), Gilbert (1927, 1928 *a*, *b*, *c*), Elliott (1916), Sanderson (1922), and others on the morphology, life history, and nuclear phenomena in these forms have given us a reasonably intimate knowledge of the group.

The Myxomycetes correspond with the Acrasieae and Labyrinthuleae in that in all three, a vegetative phase, in which the organism moves and feeds, alternates with a fruiting phase in which it is quiescent. The Myxomycetes in the fruiting phase form definite spores, the walls of which have been found in some genera at least to be composed of cellulose. In germination the spore frees one or more naked uninucleate protoplasts. The number is usually one, but in several species (Gilbert, 1928 *b*: 350) is variable (1–4), and in *Ceratiomyxa* is said to be eight. These protoplasts emerge as swarmspores. Though naked, and to a degree amoeboid, especially at the posterior end, they are provided with a **cilium (flagellum)** at the anterior end which lashes about and gives the cell a peculiar, whirling, dancing motion. In a few cases cells are found to be provided with a pair of cilia at the forward end (Gilbert 1927). After swimming for a time as swarmspores the cells usually lose their cilia and crawl about by amoeboid movements. They are then termed **myxamoebae.** Both in the ciliate and amoeboid states the cell is capable of ingesting solid food (Gilbert 1928 *a*, *c*), and in either state a temporary encystment of the individual to form a **microcyst** may result from drying out in an unfavorable environment.

These microcysts lack a definite wall, and, on the return of satisfactory conditions, revive and resume their activity.

Both the swarmspores and myxamoebae, as they feed and grow, normally multiply by repeated divisions. Finally they are attracted toward each other, and tend to coalesce. In the older literature multiple fusion of many such cells to form a multinucleate mass is described. Cienkowski first applied the term **plasmodium** to the multinucleate naked thallus thus formed. The character of the impulse which draws the cells together was not understood, but the coalescence was believed to be vegetative in character.

Recently certain workers (Gilbert 1928 *a*, in *Dictydiaethalium;* Skupiénski 1928, in *Didymium;* Wilson and Cadman 1928, in *Reticularia*) have regarded the fusion as in part sexual, and have reported fusion of uninucleate cells (**gametes**) in pairs to form **zygotes** as the first step in plasmodium formation. After the zygote is formed it may fuse with other gametes, with zoospores, or with other zygotes. According to Gilbert and Skupiénski a plurinucleate thallus thus results. In *Reticularia*, according to Wilson and Cadman, ciliate gametes fuse in pairs, myxamoebae being unknown. The zygote thus formed acts as a center of attraction toward which other ciliate haploid cells (gametes or swarmspores) are drawn. These incoming cells enter the cytoplasm of the zygote and are completely digested there, the phenomenon being regarded as of the nature of ingestion rather than coalescence. Finally the original pair of gametic nuclei fuse to form the nucleus of the zygote, and it by repeated divisions furnishes the nuclei for the growing thallus. If this account is correct the mature thallus of this species is hardly a plasmodium in the sense of Cienkowski. Since the plasmodium has, however, so long been regarded as distinctive of the Myxomycetes verification of the account must precede its general acceptance. Much additional work on the nuclear history of the group is desirable. In any case, the plasmodium is characteristic in aspect, and the phenomenon of multiple fusion, however interpreted, is admittedly confined to the slime moulds.

The plasmodium may multiply by fragmentation, or may increase in size by fusion with other plasmodia or myxamoebae. If conditions are unfavorable it may encyst temporarily to form a **sclerotium.** Normally the plasmodium is an actively growing body with the power of amoeboid movement. It is multinucle-

ate and its nuclei increase in number by mitosis as it feeds and enlarges. As it passes over or through the substratum it ingests particles of bark, bits of dead leaves, and other debris often in sufficient amount to cause a change in its color. These are taken in, the available food assimilated, and the refuse material usually ejected in the wake of the moving plasmodium. Practically all the species live a purely saprophytic existence, but some are capable of enveloping and dissolving living materials such as the fruit bodies of higher fungi. The growing plasmodium has a consistency similar to that of egg albumen. In color it ranges from pearly white through shades of cream, yellow, and orange, to red, brown, or violet. The color is to a degree definite in a given species, but it changes from day to day due to metabolic processes and is dependent somewhat on the amount of unassimilated materials present in the cytoplasm. When the plasmodium lies on the surface of the substratum it may form a thin film of irregular outline, but when permeating the crevices of a decaying log it becomes a much branched network of strands.

After an extended period of vegetative activity the plasmodium flows out upon an exposed surface, and contracts into a cushion-shaped mass. It is then ready for transformation into the fruiting phase. The Myxomycetes are split into two primary subdivisions on the basis of the character of the fructification which is then formed. In the Exosporeae, including only the genus *Ceratiomyxa*, the fruiting structure is columnar and bears spores over its outer surface, each at the end of a minute sterigma. In the Myxogastres the spores are borne inside the fructification. It is usually then called the **sporangium.** If the sporangium is irregular or sinuous in form it is termed a **plasmodiocarp.** If several imperfectly delimited sporangia become partially fused and develop into a compound fructification it is called an **aethalium.** It will be sufficient here to describe the development of the typical sporangium.

Over the surface of the cushion-shaped plasmodium the protoplasm is pushed up at numerous points to form definite papillae. These soon elongate into tiny columns, each of which develops into a sporangium. The base of each column contracts, and, in species having stipitate sporangia, forms a slender tubular stalk through which the protoplasm passes upward into an enlarging inflated terminal vesicle that later contains the spores. As the protoplasm advances refuse material is thrown out, and

is used to form a membrane, the **peridium**, over the surface of the sporangium. Similarly, as the protoplasm passes into the sporangia other waste materials are often left behind on the substratum and may form a glistening film, termed the **hypothallus.** Within the sporangium lines of cleavage cut the protoplasm into progressively smaller portions until finally uninucleate bits are delimited. Each of these secretes a definite wall, and develops into a globose spore. During the process of protoplasmic cleavage, waste materials not used in the formation of the peridium are deposited in elongate vacuoles, and form there cylindrical threads called **capillitium.** These threads are often ornamented with beautiful surface markings, spiral thickenings, spines, etc., which afford characters of diagnostic value useful in generic separation. At maturity the peridium bursts or disintegrates, and the mass of capillitium and spores is exposed. The spores then fall out and are disseminated by the wind.

The name Myxogastres was selected as indicative of the marked resemblance which certain of these organisms show to the Gastromycetes. The similarity is, however, only superficial. The capillitium and peridium in the Gastromycetes are formed from hyphae, made up of living cells, and are consequently wholly unlike the structures bearing the same names in this group.

Nuclear division in the Myxomycetes has been studied in various genera, and seems to be essentially a typical mitosis. No evidence of the existence in the group of a primitive type of mitosis resembling that of the Plasmodiophoraceae has been found. In *Ceratiomyxa*, sole representative of the Exosporeae, Olive (1907) states that a sexual fusion of nuclei in pairs occurs just preceding the cutting out of the young uninucleate spores. He says that this is followed immediately by synapsis and the reduction divisions, the mature spores being quadrinucleate. Jahn (1907) in a study of the same species found fusion and reduction at a much earlier stage. A reinvestigation of this form and a comparison of the nuclear history here with that in various members of the Myxogastres is desirable. Until we know more concerning sexuality and nuclear phenomena in the group we cannot arrive at any safe conclusion concerning its relationships with other lower forms.

Acrasieae.—The Acrasieae comprise a small group of saprophytic, and for the most part coprophilous organisms, lying apparently at the extreme lower limit of the plant world. They

have been regarded by van Tieghem, de Bary, Zopf, Harper, Olive, and others as belonging near the Myxomycetes, and are here so treated, though the differences between the two groups are at least as pronounced as their points of similarity.

In the Acrasieae the organism exists during the vegetative phase in the form of naked amoeboid cells (myxamoebae). These never pass into the ciliate swarmspore condition which, at certain periods, characterizes the motile cells of the Myxomycetes. They crawl about over the substratum, ingesting and feeding on solid materials, and increase greatly in number by repeated divisions. At the close of the vegetative period under the influence of some unexplained impulse, they move toward common centers and collect into definite colonies which have been termed by some writers **pseudoplasmodia** or **aggregation-plasmodia.** The myxamoebae composing these colonies do not fuse. Each cell retains its individuality throughout the further development of the colony and the subsequent formation of the mature fructification. The myxamoebae crawl over one another and become heaped up to form sessile or stalked masses of definite form, which in some species exhibit considerable complexity. Each cell then usually assumes a cellulose wall and becomes a spore. In two genera (*Sappinia, Guttulinopsis*) a wall is not formed, but the peripheral protoplasm is hardened into a protective layer. The cell in such cases is called a **pseudospore.** These spores or pseudospores lie in a definite mass, being held together by a mucous substance, and constitute the fructification. These masses have a superficial resemblance to the colonies of bacterial cells formed in the Myxobacteriaceae. At the close of a period of rest the spores germinate by cracking open, and the content of each escapes as a vegetative myxamoeba. The pseudospores pass into the vegetative phase gradually without casting off a membrane of any sort. Under unfavorable environmental conditions myxamoebae may enter the resting condition isolated from one another as **microcysts.**

Though the Acrasieae resemble the Myxomycetes in possessing a naked amoeboid phase, their vegetative period includes neither the swarmspores nor the true plasmodium of that group. Moreover, there is no condition which shows any resemblance to the net-plasmodium of the Labyrinthuleae. In the Acrasieae the vegetative stage ends when formation of the pseudoplasmodium begins. The latter is, therefore, a structure connected

with the phenomenon of fructification, and cannot be regarded as homologous with either the true plasmodium of the Myxomycetes or the net-plasmodium of the Labyrinthuleae.

For details of the taxonomy of the group the student is referred to the papers of Olive (1901: 1902). The families and genera recognized by him as comprising the group are as follows:

Acrasieae van Tieghem, 1880.
  Sappiniaceae
    Sappinia Dangeard, 1896.
  Guttulinaceae
    Guttulinopsis Olive, 1901.
    Guttulina Cienkowski, 1873.
  Dictyosteliaceae
    Acrasis van Tieghem, 1880.
    Dictyostelium Brefeld, 1869.
    Polysphondylium Brefeld, 1884.
    Coenonia van Tieghem, 1884.

The group as treated by Olive contains about twenty species. Prior to the appearance of his papers only one species had been reported for North America. He grew a number of forms in pure culture on solid media and in nutrient decoctions. He also studied stained preparations, and figures nuclei. No indication of nuclear fusion was observed. If sexuality exists in the group it is as yet undiscovered.

Labyrinthuleae.—This group, founded by Cienkowski (1867), is composed of a small number of very primitive and imperfectly known organisms characterized by the presence in the vegetative phase of a peculiar structure termed a net-plasmodium. This was thought by Zopf (1892) to constitute a vegetative condition intermediate in character between the aggregation-plasmodium of the Acrasieae and the true plasmodium of the Myxomycetes. He erected the group Sorophoreae to include the Acrasieae and Labyrinthuleae. As now understood the Labyrinthuleae embrace two genera, *Labyrinthula* Cienkowski (1867) with three species parasitic on algae, and *Diplophrys* Barker (1868) with one coprophilous species and another doubtful form said to be aquatic.

In the beginning of the vegetative phase the Labyrinthuleae exist as motile fusiform (spindle-shaped) cells, each of which is provided with two radiating tufts of delicate pseudopodia situated at the opposite poles. These cells may remain separate, but when they come in contact their pseudopodia usually fuse.

Anastomosis of several individuals in this fashion results in the formation of the characteristic net-like structure designated by Zopf the net-plasmodium. The fusiform individuals possess a limited degree of contractility, but retain their individuality. They appear to glide along the threads of the net, and are thus limited in their wanderings. During this period of activity they feed, increase in size, and undergo repeated division. In division the cell elongates, is constricted at the middle, and is finally pulled apart into two new individuals held together by a plasma strand. The research of Zopf on *Labyrinthula* indicated that food is obtained in solution rather than in the solid condition.

At the close of the vegetative period the wandering cells collect into sessile or stalked masses, and pass into an encysted state which may be termed the fructification. The individual cells in *Labyrinthula* assume definite walls and are termed spores. The chemical composition of the wall is apparently unknown. In *Diplophrys* a wall is absent, and the cell is called by Olive (1901) a pseudospore. After a period of rest, the organism passes again into the vegetative phase, the spores in germination freeing one to four of the fusiform cells provided with polar pseudopodia.

The Labyrinthuleae are far less well known than the Acrasieae. The species of *Labyrinthula* have been observed only by their authors Cienkowski and Zopf, while those of *Diplophrys* have been very inadequately studied. The position of the group in the classification is extremely doubtful. Many zoologists include it in the Protozoa. The type of cell division seems to indicate a relationship with the Monadineae of that group. The net-plasmodium has only a superficial resemblance to the true plasmodium of the Myxomycetes, and it is unlikely that the Labyrinthuleae are more than remotely related to them.

Fungi.—The essential characters of the other groups of the Thallophyta having been indicated above, the field is now cleared for a general consideration of the fungi. This must of necessity be somewhat more brief than would seem from certain points of view desirable.

The fungi constitute by far the largest and most diverse group of non-chlorophyll containing thallophytes. In general they may be said to differ from other colorless forms in the possession of the filamentous vegetative structure known as

mycelium. The **spores** of the fungi are of many types, but in practically all cases in germination they put out one or more small protuberances which elongate and assume the form of more or less cylindrical threads. These are termed **germ tubes.** As they increase in length they tend to branch, and soon a much branched complex of threads constituting the vegetative plant body or thallus is formed. On account of its mould-like aspect in some groups this structure received the name mycelium. A single thread or branch is termed a **hypha** (plur. **hyphae**). In some fungi the development of mycelium is very limited (*e.g.*, Saccharomycetaceae) and in a few groups (Olpidiaceae, Woroninaceae, Synchytriaceae, Ancylistaceae) the thallus may fail completely to assume the filamentous form. In such cases mycelium is said to be absent. In some of the algae, threads comparable to mycelium are present. In certain bacteria, moreover, the cells remain together in chains forming long threads which are analogous to mycelium. The fungi which lack mycelium resemble the other members of the group in the characters of their reproductive processes, and in general are not easily confused with other lower thallophytes. A few (Plasmodiophoraceae, Woroninaceae) approach the Myxomycetes, and correspond with them in that the thallus is a naked protoplast at least in early stages. In the higher fungi a cell wall is always present, and is composed of a modification of cellulose, termed fungus cellulose, which in composition is akin to chitin. In the lower fungi the wall in many forms gives the reaction for true cellulose. Though green plants in general store their food reserve in the form of starch this substance is unknown in the fungi. Instead, the soluble food is transformed into an oil, glycogen, and is stored in the vacuoles. In this connection a consideration of the taxonomic position of the genus *Rhodochytrium* Lagerheim, containing a single species *R. spilanthidis* parasitic on ragweed (*Ambrosia spp.*), is of interest. This organism lacks chlorophyll but stores as starch the food obtained in soluble form from the host. In morphology it corresponds closely with the algal genus *Phyllobium* Klebs (1881). Because it lacks chlorophyll Lindau (1899) places it in the fungi. Other students (Lagerheim 1893; Atkinson 1908 *a*, *b*) incorporate it in the algae. This difference in point of view illustrates the difficulty of drawing a sharp line between the two groups. The green algal genus *Chlamydomonas*, which in certain classifications embraces some non-chlorophyll con-

taining saprophytic forms, constitutes another illustration of the point. Such border line cases make difficult precise generalizations concerning the limits of the fungi.

The reproductive processes of most of the fungi are far more highly developed than those of any of the bacteria or slime thallophytes. They are approximated in complexity in some of the algae. Many of the fungi, apparently the majority, are polymorphic, *i.e.*, form two or more kinds of spores in the life cycle. These different spore forms are designated either as perfect or imperfect. The perfect spore form occurs more or less definitely in connection with the sexual process, and is often called the sexual spore. The imperfect spore form is asexual. More than one type of asexual spore may be developed in a single species. The sexual and asexual spores are often borne together or in succession on the same thallus, but in some cases occur on different thalli. Unless borne together the genetic connection between the two may remain for a long time unsuspected. The phase of the life cycle in which the perfect spore form occurs is termed the perfect or sexual stage. That in which the imperfect spore form is developed is called the imperfect or asexual stage. In both cases, especially in the higher fungi, the spores are often borne in definite aggregations or conceptacles termed in general fruit bodies.

In as far as possible, the classification of the fungi is based on the characters of the perfect stage. In practically all modern systems of classification the fungi are subdivided on this basis into three major natural groups,—Phycomycetes, Ascomycetes, and Basidiomycetes. These subdivisions usually rank as classes, are coordinate, are treated as units in the phylogenetic arrangement, and are separated rather sharply from one another. In these respects they differ essentially from the group Fungi Imperfecti, which is usually appended to them as a fourth major subdivision of the fungi. This group was erected for the temporary accommodation of the imperfect stages of fungi which have not yet been identified in connection with their perfect stages. There are many hundreds of them. They are believed to be, in most cases, imperfect stages of Ascomycetes. A smaller number probably belong with Phycomycetes or Basidiomycetes. The perfect stages of some of them may no longer occur in nature, or possibly may never have been developed. The group as a whole has no unity and consequently no proper place in a natural

system. The imperfect forms of which it consists are separated by an artificial classification based largely on spore characters. When one of them is proved to be the imperfect stage of a known member of the Phycomycetes, Ascomycetes, or Basidiomycetes it passes automatically to that group, and bears thereafter the name applied to the perfect stage. It is to be expected that in time hundreds of such transfers will be made. Certain forms, which are properly speaking Fungi Imperfecti, have never been included in the group because their characters are such as to indicate clearly their actual relationships. Members of the Mucorales known only in the asexual (sporangial) condition, and unconnected stages of rusts (Uredinales) belonging to the form genera *Aecidium*, *Cacoma*, *Peridermium*, *Roestelia*, and *Uredo* fall in this category.

The outstanding characters of the Phycomycetes, Ascomycetes, and Basidiomycetes will now be indicated briefly. The Phycomycetes embrace the lower fungi treated in this book. A general discussion of the group is given in the following chapter. The Ascomycetes and Basidiomycetes are called the higher fungi. Certain authors restrict the name Eumycetes to them.

The **Phycomycetes** viewed in their entirety are a diverse group. The primitive members of the class are chiefly aquatic, while the more recent are terrestrial. The thallus in the lower forms is characteristically simple and inconspicuous. In the higher it develops as a profusely branching mycelium, which is usually more evident than the reproductive bodies. The mycelium is usually coenocytic (non-septate and plurinucleate), but in some forms, chiefly the highest, tends to develop septa in age or may even be normally septate from the beginning. In practically all cases septa are formed in the delimitation of the reproductive cells. Sexual organs are commonly present and usually functional. The product of sexuality is usually a spore (oospore or zygospore). In a few known cases motile sex cells (gametes) fuse in pairs to form motile zygotes. In a single genus, *Monoblepharis*, ciliated antherozoids fertilize the female cell. In some species the sexual cells are no longer functional. In others, one or both cells have been suppressed. Asexual reproduction occurs typically by means of spores (sporangiospores) borne in a sac called the sporangium. The sporangiospores in the lower forms are usually motile (zoospores, swarmspores), but in the higher are usually non-motile (aplanospores). In many cases,

especially in higher groups, the sporangium germinates directly by one or more germ tubes, functioning thus in its entirety as a spore. It is then called by many writers a conidium. The most characteristic structures of the group as a whole are the sporangium, coenocytic mycelium, and zoospores.

In the **Ascomycetes** the mycelium is well developed in most cases, and is typically septate. It is usually less conspicuous, however, than the reproductive bodies, the condition in this respect being the reverse of that in the Phycomycetes. Motile cells are never formed. The group is distinguished by the **ascus,** which is a sac forming endogenous spores, usually in small and definite number (typically eight, but less frequently some other number which is usually a multiple of two). Though a sac forming endogenous spores, the ascus is not homologous with the sporangium, and differs from it in several important respects. It is sexual in character, in it two nuclei, usually regarded as sexually different, fuse, and in it reduction division occurs. Following the reduction process the **ascospores** are cut out by means of the astral rays in a peculiar process known as free cell formation. The spores thus delimited are surrounded by unused cytoplasm termed **epiplasm.** In the sporangium, epiplasm is absent, and the process of progressive cytoplasmic cleavage, which accomplishes spore formation there, is a wholly different phenomenon. In the lower Ascomycetes the asci are formed without order throughout a mould-like mycelium, or exist as isolated cells as in the yeasts. In the great majority of higher forms they are collected into a more or less spherical, flask-shaped, cup-shaped or disc-shaped fruit body, usually conspicuous and termed the **ascocarp (apothecium, perithecium).** Asexual reproduction takes place by means of spores termed conidia. **Conidia** are exogenous and are adjointed at the ends of more or less specialized hyphae called **conidiophores.** The conidium of the Ascomycetes and Basidiomycetes is regarded as homologous with that of the Phycomycetes and hence with the sporangium. The conidiophores in some forms are scattered over the mycelium. In others, they are aggregated into definite sori or fruit bodies (**acervuli, sporodochia, coremia, pycnidia**). In some forms the hyphae break apart at the septa to form unicellular asexual spores termed **oidia.** The group as a whole may be roughly split into the Discomycetes and Pyrenomycetes. It contains the yeasts, morels, cup fungi, truffles, and many forms

with minute fruit bodies. It is the largest of the three major subdivisions of the fungi, and contains about twenty orders.

In the **Basidiomycetes** the thallus exists as a well developed mycelium. The individual hyphae often lie close together and run more or less in parallel forming heavy strands or cords termed **rhizomorphs.** The fruit body usually results from differentiation at the tip of a rhizomorph. The hyphae are septate and are often provided at the septa with peculiar structures termed clamp connections. The clamp is of the nature of a curved lateral branch connecting the two cells otherwise separated by the septum, and is probably homologous with the ascus hook developed in crozier formation in the Ascomycetes. The Basidiomycetes are distinguished by the **basidium,** an organ similar to the ascus and probably homologous with it, but differing in that the spores are formed **exogenously** (outside) rather than **endogenously** (inside). The sexual nuclei fuse in the basidium and reduction occurs there. The resulting nuclei pass out of the basidium through minute sterigmata into vesicular enlargements at their tips, which then mature into spores (**basidiospores**) and are ejected into the air. Usually four spores are formed. The basidia usually arise in or on specialized fruit bodies and commonly stand side by side forming a palisade layer termed the **hymenium.** Asexual reproduction by means of conidia of various types commonly occurs. The group may be divided roughly into smuts, rusts, Hymenomycetes and Gastromycetes. It contains the mushrooms, bracket fungi, coral fungi, gelatinous fungi, stink-horns, puff-balls, bird's nest fungi and other prominent forms. It is a large group but has been more thoroughly studied than have the Ascomycetes. Sexual organs, present in many Phycomycetes and numerous Ascomycetes, are apparently absent in the Basidiomycetes. The group is characterized by a distinct alternation of generations in which a mycelium composed of uninucleate cells alternates with mycelium in which the cells are binucleate. The same type of cycle somewhat less sharply marked occurs in the Ascomycetes.

For a more detailed treatment of the Ascomycetes and Basidiomycetes, especially with regard to the problems of comparative morphology and cytology, the student is referred to the recently published books of Gwynne-Vaughan (1922) and Gäumann and Dodge (1928). The taxonomic literature is extensive and

widely scattered, and the systematist is dependent to a large degree on the Sylloge Fungorum of Saccardo and the various lists and abstracting journals which lead him to the original papers.

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CHAPTER II

PHYCOMYCETES

The name Phycomycetes, translated literally, means **algal fungi.** It was first applied by early investigators, who recognized that members of the group resemble strikingly in essential features of morphology certain of the green algae.

Origin of the Phycomycetes.—Several prominent early mycologists and algologists believed that the Phycomycetes are merely degenerate algae, which, coincident with the assumption of the parasitic or saprophytic habit, have lost their ability to form chlorophyll. Pringsheim (1858), one of the first students of note on aquatic Phycomycetes, interpolated the genera of the Saprolegniales among those of the siphonaceous green algae. Following his lead Cohn (1872) and Sachs (1874) proposed classifications in which all the known families of the fungi are scattered among those of the algae. In the arrangement presented by Sachs, the Chytridiales are grouped with the Protococcoideae, the Oomycetes with the Oosporeae, the Zygomycetes with the Conjugatae, and the Ascomycetes and Basidiomycetes with the Florideae (red algae). These writers felt that the change to the parasitic or saprophytic mode of life, accompanied by the loss of ability to form chlorophyll, had occurred at various points along the algal line. They believed that several series of non-chlorophyll bearing forms had been thus initiated. Consequently, to them there seemed to be no logical basis in a phylogenetic arrangement for segregation of the colorless forms as a separate group. This point of view was generally accepted at the time, and is still held by some students. Its correctness was first seriously questioned by de Bary (1881). That great student of mycology agreed that, by interpolation of the colorless forms among the green, a usable arrangement had been devised, but he doubted that it constitutes a natural system. He believed that each of the principal subdivisions of both the fungi and algae has its own lower and higher forms, and argued that the

higher members of any one group show relationship with the lower members of the groups above. He felt that any attempt to merge the two series would necessarily result in the dismemberment of both. Since the physiological processes of organisms possessing chlorophyll are very different from those of forms in which it is lacking, it seemed highly unlikely to him that the change from one type of metabolism to the other had occurred at a number of different points along the algal line. He concluded finally that the algae and fungi probably arose as separate groups very early from unicellular chlorophyll bearing and non-chlorophyll bearing organisms respectively, and have subsequently evolved along more or less parallel lines. The rather constant environmental conditions characterizing the aquatic habit has been offered in explanation of the development of similar structures in the two series.

The two opposing points of view have persisted with minor alterations to the present day. In most standard taxonomic works the ideas of de Bary have prevailed, and the algae and fungi are treated as separate groups. In America, the teachings of Sachs were elaborated by one of his students, Charles Bessey (1907; 1914), at the University of Nebraska, and the interpolation of the fungi in the algal series constitutes an outstanding feature of the system of classification used by the Bessey school of botanists (Ernst Bessey 1913). Certain other students of the cryptogams who agree in regarding the fungi as degenerate algae are content for convenience sake to have the two groups treated taxonomically as distinct.

In recent years de Bary's suggestion that the two series have evolved in parallel has been championed by various students (Vuillemin, 1912). In America this point of view was given prominence by Atkinson (1909; 1915). He presents the evidence indicating that the fungi have in fact no connection with the algal line, but instead have been derived from primitive colorless organisms below the level of the existing Chytridiales. He emphasizes the fact that in a number of points of morphology and behavior the lower fungi resemble the higher, and differ from the algae. He contrasts the zoospores of the fungi with those of the algae, finds in the Chytridiales the origin of the phenomena of diplanetism of swarmspores and proliferation of sporangia characteristic of some of the Saprolegniales, sees in certain of the Chytridiales and Ancylistales the origin of the

peculiar type of sporangial germination present in *Pythium*, emphasizes the fact that the sexual organs of the Oomycetes in general function quite differently from those of the siphonaceous green algae, argues that the Ascomycetes and Basidiomycetes are connected with the higher Phycomycetes through such forms as *Endogone* and *Dipodascus*, and combats the point of view that the higher fungi arose from the red algae. The student interested in the detailed argument is referred to the papers of Atkinson and to others cited in his bibliographies. An adequate elaboration of the subject here does not seem desirable. The writer, who was a student under Atkinson, is inclined to accept in the main his point of view on the phylogeny of the fungi, and feels, moreover, that, as more critical and comprehensive work is done on the various groups of lower organisms, a greater body of evidence will be assembled justifying it.

Thallus.—Generalizations concerning the morphology of the Phycomycetes are difficult on account of the great diversity of the group. The vegetative portion of the plant in the primitive members of the class is inconspicuous and simple. In the higher forms it develops into a profusely branching and extensive mycelium. Though the mycelium in the group as a whole is characteristically **coenocytic** (*i.e.*, non-septate and plurinucleate), in some of the higher families septa are commonly present. In the Mucorales they are found usually only in old hyphae. In the Entomophthorales their formation occurs in most forms rather early. Even in typically coenocytic thalli septa are almost invariably formed in the delimitation of the reproductive cells (sporangia, antheridia, and oogonia). In certain lower groups (*e.g.*, Cladochytriaceae) the mycelium is often evanescent. In the Entomophthorales it commonly falls apart at the septa into the component cells.

When the mycelium is coenocytic it is considered by many writers to be a single cell regardless of its extent or the profusion of its branching. Others regard each nucleus with the immediately adjacent enveloping cytoplasm as constituting a cell. An interesting application of the latter point of view is seen in the use of the term **gametes** for the nuclei of the plurinucleate sexual organs (**coenogametes**) of this group. Regardless of the interpretation accepted, it is known that the cytoplasm and nuclei commonly flow throughout the thallus, and there is apparently no basis for an assumption that definite portions of

the cytoplasm maintain a constant and intimate association with individual nuclei.

The thallus of the Phycomycetes is usually provided with a membrane or wall, but in some of the lower groups (Plasmodiophoraceae, Woroninaceae) it is naked throughout all or the major portion of its existence. Although the wall in the majority of the fungi is composed of fungus cellulose (a substance resembling chitin), in certain members of the Phycomycetes it gives the reaction for pure cellulose.

In some of the lower families the entire thallus is transformed at maturity into a single reproductive organ (Olpidiaceae) or group (**sorus**) of them (Synchytriaceae). In such cases the organism is said to be **holocarpic.** In the higher families, only a portion of the thallus is transformed for purposes of reproduction, and the remainder continues to function vegetatively. Such organisms are termed **eucarpic.** In species developing abundant mycelium the reproductive bodies are relatively less conspicuous than the thallus. Prominent compound fructifications, comparable to those of the Ascomycetes and Basidiomycetes, are almost wholly absent. A tendency toward the formation of such structures is present in the Mucorales in *Endogone* and to a lesser degree in *Mortierella.*

Asexual Reproduction.—In the Phycomycetes asexual reproduction occurs in most cases by means of spores (**sporangiospores**) borne in unicellular sacs called **sporangia.** In the lower orders, the sporangiospores are usually naked and motile and are termed **zoospores.** In the higher, they are non-motile, have definite membranes, and may be designated as **aplanospores.** Though in a few of the lowest forms the zoospores are amoeboid, they are usually ciliate and may then be called **swarmspores.** In most of the families of the lowest order (Chytridiales) they are uniciliate, but in the single family Woroninaceae of that order and in almost all cases in higher groups they are biciliate. When biciliate, the two cilia arise from the same point on the swarmspore. In some genera, one cilium is markedly longer than the other. The swarmspore is usually either pyriform (pear-shaped) or reniform (bean-shaped), the cilia being attached at the narrowed end in the former case and at the lateral depression (hilum) in the latter. Zoospores are characteristic of the more primitive genera, and are indicative of an aquatic or semi-aquatic habit. When present in terrestrial forms they swim in soil water or on

the surfaces of hosts wet with rain or dew. Zoospores are not found in groups above the level of the Peronosporales. They are wholly absent in the Zygomycetes, Ascomycetes, and Basidiomycetes.

The number of spores formed in the sporangium is almost universally indefinite, but in a few genera is characteristically one or two. In the group as a whole it is extremely various (often several hundred), and is chiefly dependent upon the number of nuclei which chance to flow in from the thallus below. The sporangium in its asexual character, and in the indefinite number of its spores differs strikingly from the ascus. Moreover, while in the ascus the spores are delimited by the astral rays, in the sporangium successive cleavage planes traverse the cytoplasm and in a wholly indefinite fashion finally cut it into bits which are usually uninucleate. These then round up into spores. There remains no intersporal cytoplasm such as characterizes the ascus. The essential differences between spore formation in sporangium and ascus are indicated by Harper (1899) and Swingle (1903).

The hypha on which the sporangium is borne is differentiated in many genera as a definite stalk termed the **sporangiophore.** In some groups, it is specialized in form and may be characteristically branched.

If the sporangium forms zoospores, it is called a **zoosporangium.** If the spores are ciliated, it may be called a **swarmsporangium.** Zoospores in some forms escape from the sporangium through a pore or exit tube of definite form and position. In others, the sporangial wall disintegrates or bursts in an indefinite fashion. After a period of motility the zoospores commonly assume the spherical form and become enveloped in a definite membrane. Usually they then put out one or more germ tubes and germinate directly into mycelium. In those lower forms in which mycelium is absent, the zoospore merely enlarges and with or without the assumption of a membrane develops directly into the thallus. Aplanospores are chiefly wind borne. They escape from the sporangium usually by the disintegration of its wall and in germination form germ tubes.

In many cases in the Phycomycetes, especially in the higher groups, there are found asexual reproductive cells which correspond in size and form with the sporangia, are unquestionably

homologous with them, and differ only in failing to develop endogenous spores. These cells function at maturity in their entirety as single spores and germinate by one or more germ tubes. Such reproductive cells correspond morphologically to the **conidia** of the higher fungi and this term is often applied to them.

The conidium of the higher fungi is an asexual spore. It is usually cut off from a definite **conidiophore,** is deciduous, is typically wind borne, and germinates by one or more germ tubes, never by endogenous spores. In many of the higher Phycomycetes (*e.g.*, *Peronospora*, *Cunninghamella*, *Empusa*) the asexual reproductive cells have all of these features. In other forms (*e.g.*, *Saprolegnia*, *Mucor*) they have the characteristics of the typical sporangium, being persistent instead of deciduous and germinating by endogenous spores instead of by germ tubes. In intermediate types they are deciduous but germinate by endogenous spores (*e.g.*, *Phytophthora*, *Pilobolus*), or are persistent but germinate by germ tube, as in some cases in *Pythium*. Furthermore, forms exist (*e.g.*, *Phytophthora*, *Plasmopara*) in which the type of germination is unstable and dependent on environmental factors. In such forms two asexual cells identical in aspect and borne on the same hypha may be induced to germinate differently (one by germ tube, the other by endogenous spores) in an experiment in which different temperatures are provided. Consideration of these facts make it evident that precision in the application of the terms sporangium and conidium in the Phycomycetes is extremely difficult of attainment. In species in which the type of germination is fixed the terms may be used without ambiguity, if their limits be first arbitrarily defined, though all writers will not agree as to their limits. In cases in which the method of germination is dependent on environmental factors selection of the name must be deferred until germination has actually occurred. Even then it is sometimes necessary to designate either as sporangiophore or conidiophore, a structure on which both sporangia and conidia have been borne.

In the present volume, the writer has attempted to avoid confusion by restricting application of the term conidium in the Phycomycetes to the Zygomycetes. This procedure is purely arbitrary. The border line conditions which exist in the Zygomycetes are less confusing than those in the lower groups,

and it is possible to use the terms sporangium and conidium together there with less difficulty.

The transition from the typical persistent sporangium of the lower Phycomycetes to the deciduous conidium of the higher has been accomplished in various ways in different groups. While in the Peronosporales the transition has been marked by a rather abrupt change from the swarmspore type of germination to the germ tube type, in the Mucorales gradual and pronounced changes in morphology have occurred. In the latter order the sporangium has tended to decrease in size, to become few-spored, and to fall away. The small few-spored sporangia thus resulting have been termed **sporangiola.** In some cases they are monosporic, the wall of the spore being clearly discernible within that of the sporangiolum. In their highest development, the spore wall fails to form, and the whole cell is then termed a conidium.

In various genera of the Phycomycetes (*e.g.*, *Saprolegnia*, *Mucor*) an additional asexual spore form is present, which cannot be clearly homologized with the sporangium. These spores have been termed **chlamydospores** or **gemmae.** They occur chiefly on old thalli, and are essentially merely vegetative cells with thickened walls. Similar spores are not uncommon among the higher fungi. They function as resting spores and germinate by germ tube. They are more often intercalary than terminal, and usually are not deciduous.

Sexual Reproduction.—A comprehensive general discussion of the phenomena of sexuality in the Phycomycetes must of necessity be somewhat detailed. Broad general statements are impossible on account of the great variation within the group. Several distinct types of sexuality occur, and a consideration of their relationships is important in connection with questions of phylogeny and classification.

The simplest form of sexuality represented is that in which swarmspore-like cells, called **gametes,** fuse in pairs to form motile **zygotes.** Because the fusing cells are motile the process is termed **planogamic copulation.** As they are morphologically indistinguishable it may be called also **isogamy.** This is probably the ancestral type of sexuality in the group. It persists today in a few known cases, *e.g.*, *Olpidium viciae* (p. 75) and *Synchytrium endobioticum* (p. 82), and perhaps is present in a considerable number of other incompletely investigated members of the

Chytridiales, especially those having resting spores of unknown origin. This type of sexual process probably originated very early in the copulation of swarm cells in species in which such cells had functioned previously only asexually as swarmspores. In the relatively few present-day Phycomycetes in which such swarm cells fuse as gametes, there occur in the life cycle other cells of identical aspect which still function as swarmspores. The rather meager data gained from observations indicate that the three sorts of swarm cells (swarmspores, male gametes, and female gametes) are delimited in different parent cells. The cell in which the swarmspores are borne is called the sporangium. Those in which the gametes are formed are termed respectively the male and female gametangia. The three sorts of parent cells are morphologically indistinguishable. Considerable evidence indicates that during the period of active growth while the food supply is abundant and other conditions favorable the fungus forms several successive generations of swarmspores, and that when conditions become unfavorable and the rest period is approached gametes are produced instead. In parasitic species, infection of the host is accomplished by either swarmspores or zygotes. After the gametes fuse the zygote (**planozygote**) is motile for a time, but finally comes to rest, rounds up, increases considerably in size, and at maturity develops into the **resting spore.** As the resting spore in germination frees swarmspores, it may be termed also the **resting sporangium.** The term **zygospore,** used for similar structures in certain algae, is avoided here since it has become fixed in its application in a different sense in the group of higher Phycomycetes called the Zygomycetes.

As has been indicated above the species representative of this type of sexuality are termed **isogamic,** because the fusing gametes are alike. They may be called also **isogametangic** in that their gametangia are indistinguishable. Though no isogamic species known at present are **heterogametangic** it is possible that future investigations will bring to light forms of that type also.

In those Phycomycetes in which planogamic copulation of like gametes occurs, the fusing cells and the resultant zygote are usually both ciliate. However, in a single imperfectly known species, described by Griggs (p. 75) under the name *Monochytrium stevensianum* the gametes are non-ciliate and fuse in the amoeboid condition. Moreover, in two species of *Olpidium,*

segregated long ago by Fisch (p. 75) under the generic name *Reesia*, though the gametes are ciliate, the zygote is finally non-ciliate and amoeboid. Such forms may be regarded, perhaps, as representing transition conditions from the more primitive type of sexuality where the fusing cells are ciliate to the more recent types in which they are wholly non-motile.

Planogamic copulation between cells dissimilar in size and shape was unknown in the fungi until very recently, when it was discovered by Kniep (p. 132) in *Allomyces javanicus* of the Blastocladiaceae. In this species uniciliate gametes, differing considerably and constantly in size, fuse to form a biciliate zygote. The zygote swims for a time, but soon invests itself in a membrane, and puts out a germ tube which develops directly into the rhizoid system comprising the young thallus. This species in addition to being **heterogamic (anisogamic)** is also **heterogametangic.** The gametangia, though of essentially the same form, are of two sizes. The smaller always contains the smaller gametes, while the larger contains the larger ones. Influenced by the situation in other higher Phycomycetes, Kniep regards the smaller gametangium as male and the larger as female, and designates the two as **antheridium** and **oogonium** respectively. As the larger gametes are formed in the larger gametangium, it must be admitted that the only criteria available for a determination of the sexual identity of these structures indicate that they are female. Nevertheless, the possibility remains that they are not. Though isogamic-heterogametangic or heterogamic-isogametangic members of the Phycomycetes with planogamic copulation have not been discovered, it is clear that the determination of sexual identity on the basis of size alone would be even more questionable in such cases. It is possible, moreover, that heterogamic-heterogametangic species with planogamic copulation may be found in which the smaller gametes are borne in the larger gametangium and the larger gametes in the smaller. Even admitting that these hypothetical types may be, in fact, wholly absent in the group it will be agreed that every effort should be made to attain uniformity and precision in the application of terms. To this end the writer prefers to avoid the use of the names oogonium and antheridium in this lower form in which both gametes are motile. If the larger gamete in *Allomyces javanicus* be admitted to be the female then the type of sexuality existing in this isolated case

may fairly be regarded as intermediate between the planogamic copulation of isogametes in *Olpidium* or *Synchytrium*, and heterogamic copulation as it exists in *Monoblepharis* where the female gamete is practically non-motile and spherical. Since in other respects the Blastocladiaceae and Monoblepharidaceae are clearly closely related a similarity in their sexual process is not surprising.

The type of heterogamic copulation represented by *Monoblepharis* is clearly higher than that in *Allomyces* in that the gametes are easily distinguishable as male and female respectively. They are not merely dissimilar in size. They differ in other respects as well. From the beginning the female gametangium is uninucleate. Finally its contents contract to form a single, large, spherical, naked, non-ciliate and practically non-motile gamete, which is here called the **oosphere.** The male gametangium is smaller than the female and of a somewhat different shape. At maturity it frees several uninucleate, uniciliate gametes. These swim about actively and are attracted to the oosphere. They are termed **antherozoids (sperms, spermatozoids).** An antherozoid, on coming in contact with the oosphere, fuses with it, and its nucleus approaches and unites with the female nucleus. This fusion of the sexual nuclei is termed **fertilization,** and the female nucleus is said to have been fertilized. Following fertilization the oosphere assumes a wall, and thereafter is called the **oospore.** The oospore functions as a resting spore, and, after a period of quiescence, puts out a germ tube which develops into a new thallus.

The female character of the oosphere is evident in that it is functionally the receiving cell, remaining passive until approached and fertilized by the male gamete, and in that it has, thereafter, the capacity for developing into the new plant. The gametangium which bears the oosphere is from that fact alone clearly the female, and may be called without hesitation the oogonium. The antherozoids are surely male in that they effect fertilization of the oospheres. The gametangium in which they are formed is consequently male and is termed the antheridium. The larger size of the female gamete and gametangium is pronounced and corresponds in general with the situation in all higher oospore-forming Phycomycetes. *Monoblepharis* is noteworthy in that it is the only genus of the known Phycomycetes in which ciliate male gametes fertilize

the oosphere. It is unique also in that the terms oosphere and female gamete may be applied here with complete justification to the same body.

In many other genera of the Phycomycetes fertilization is immediately preceded or accompanied by a differentiation of the contents of the female gametangium to form one or more spherical masses of protoplasm. Though these are commonly called oospheres they are not completely homologous with the oosphere of *Monoblepharis*, since they are in the beginning multinucleate. Phycomycetes having oospheres of this sort include such genera as *Achlya*, *Dictyuchus*, *Pythium*, *Albugo*, and *Peronospora*. In no case of this type does the male gametangium form antherozoids. Instead it pushes out a branch, called the **fertilization tube,** which pierces the wall of the female gametangium and penetrates to the oosphere before rupturing and discharging a part or all of its contents. When the oogonium contains several oospheres the tube branches, or several antheridia may send tubes into a single oogonium. In all such cases the male and female gametangia are both plurinucleate from the first. In the more primitive genera (*e.g.*, *Achlya* and *Dictyuchus*) the entire content of the oogonium is used in the formation of the oospheres, whether there be one or more. In higher forms (*e.g.*, *Albugo*, *Pythium*, *Araiospora*, and *Peronospora*) differentiation of the protoplasm into **periplasm** and **ooplasm** occurs, and only the ooplasm is incorporated in the single oosphere formed in these genera. The oosphere in the beginning is plurinucleate. Later it usually becomes uninucleate, through disintegration of the extra (**supernumerary**) nuclei, before fertilization occurs. In a few species (*e.g.*, *Albugo bliti*) the oosphere remains plurinucleate and, when fully formed, is fertilized by a number of male nuclei which are discharged from the fertilization tube and fuse in pairs with the female nuclei. Even in the forms in which the plurinucleate oosphere becomes uninucleate before fertilization the body may not be correctly termed a gamete except with respect to function since in the morphological and phylogenetic senses several potential gametes contribute to the formation of each oosphere. In species in which the oosphere remains plurinucleate to maturity the terms **compound** oosphere and **coenogamete** have been applied by various authors. To the student of comparative morphology the latter name seems especially unfortunate. The

nuclei which fuse here are clearly in their homologies the gametic nuclei, and it may well be said that here fusion of undifferentiated gametes occurs. The oosphere in such cases is thus not comparable morphologically to the gamete in *Monoblepharis* but is instead an aggregation of non-individualized gametes functioning in its entirety as a single gamete.

The same situation exists in the case of the antheridium. In species in which the oosphere remains plurinucleate to maturity numerous antheridial nuclei function. In species in which the mature oosphere is uninucleate conditions are various. In some cases only a single male nucleus passes through the fertilization tube. In others supernumerary antheridial nuclei enter the oosphere, and, on failing to find mates, disintegrate. In some of the higher genera (Peronosporales) the content of the antheridium is differentiated into a central mass of functional **gonoplasm** which passes through the tube, and a layer of **periplasm** which remains in the antheridium. In these various cases, the antheridial nuclei, whether functional or not, are termed gametes or gametic nuclei by many writers. The term coenogamete is used by other authors, and is applied to the content of the antheridium considered as a unit. After fertilization has been effected, the antheridium tends to collapse, and is of no further significance in the life cycle. Meanwhile in the oogonium, the oosphere assumes a wall, and thereby becomes the oospore. The oospore functions as a resting spore, and finally germinates to form the thallus of the succeeding generation.

The fungi which form oospheres were called **Oomycetes** (egg-forming moulds) by early students. The name has persisted, and, in most modern classifications, is applied to one of the primary subdivisions of the Phycomycetes. The type of sexual reproduction characterized by oosphere formation is termed **oomycetous.** The term **oospore** is used correctly only for the spore which results directly from the maturation of the oosphere.

Though the delimitation of the oosphere and its transformation into the oospore are the most essential characteristics of oomycetous reproduction several other features of this type of sexuality are commonly present and should be indicated. The sexual identity of the male and female gametangia is evident. They differ in size and shape, the female being the larger and typically the more nearly globose. They differ also in function,

the male cell being more active, and contributing to the more passive and receptive female cell which then matures the oosphere. The fertilization tube, present in all forms but *Monoblepharis*, does not function as a conjugation tube. Instead of copulating with the oogonium, it pierces the oogonial wall and penetrates to the oosphere. Properly speaking, therefore, copulation between the gametangia does not take place, and as they do not merge to form a common cell their individuality is retained even after fertilization.

Contrasting in the higher Phycomycetes with oomycetous reproduction is a wholly different type of sexuality termed **zygomycetous.** It is present in many genera, and these considered as a group are called the **Zygomycetes.** In these forms differentiation of the female gametangium to form oospheres does not occur, and the end product of the sexual process is termed the **zygospore.** The male and female gametangia are usually morphologically identical, and are not designated by the names antheridium and oogonium. In a few genera (*e.g.*, *Zygorhynchus*) they show a pronounced and constant difference in size and shape, but the character of the sexual process is such that the larger cell may not be regarded with certainty as the female. Direct copulation of the gametangia takes place in all cases, the contiguous walls of the two sexual organs are absorbed, and a common cell results in which the two protoplasts are completely merged. In many genera the fusion cell then enlarges and the individuality of the copulating gametangia is completely obliterated. In other cases only a pore is formed between the two cells, and, though a fusion cell thus results, the identity of the gametangia is retained. Finally, the fusion protoplast rounds up, assumes a wall, and matures into the zygospore. In some species the spore forms within one gametangium or the other. In others it fills the common cavity resulting from their complete fusion. In still others it exists as a globose bud protruding from one of the gametangia or from their point of union. It is not clearly an endogenous spore. The gametangial wall enveloping the fusion protoplast becomes greatly thickened and when thus transformed serves as the wall of the spore. The zygospore differs from the oospore in not lying free in the gametangium. Fusion of one or more pairs of sexually different nuclei occurs in the zygospore, nuclear conditions varying apparently in different species. Functionally the zygospore corresponds with

the oospore in being a resting spore. After a period of quiescence it germinates by a germ tube.

It is evident that the zygomycetous type of reproduction differs from the oomycetous essentially in that the oosphere is lacking, and the sexual identity of the interacting gametangia is in doubt. It differs also in that true gametangial copulation occurs. As there is no oosphere the fertilization tube is unnecessary and is lacking, and the resting spore tends to fill the cell instead of lying free as in the Oomycetes.

These various features of dissimilarity considered together indicate clearly that the Oomycetes and Zygomycetes are not closely related. Though presumably at a remote period they had a common ancestry, it is evident that they represent two series of genera which have arisen in parallel from still lower forms. The probable line of development of the Oomycetes from primitive aquatic forms with planogamic copulation has been indicated above. The origin of the Zygomycete line is somewhat more obscure, though forms possessing one or more undoubted zygomycetous characters exist among the Ancylistales and Chytridiales.

In certain of these lower Phycomycetes primitive types of sexuality exist in which oomycetous and zygomycetous characters are found associated in the same species. These cases have been inadequately studied, and knowledge of them is too fragmentary to justify conclusions as to their relationships. It has long been known that in some of the Chytridiales (*e.g.*, *Olpidiopsis* and *Pseudolpidiopsis*) the resting spore is accompanied at maturity by one or more small empty appendages. Early investigators, ignorant of the real nature of these structures, called them **companion cells.** Now they are known to be emptied male cells. Though few Chytridiales having companion cells have been studied critically they are apparently all endophytic parasites, and their life history is believed to be essentially as follows. Ciliated, free-swimming swarm cells exist in the water outside the host, and in all cases function as swarmspores. There is no basis for an assumption that any of them ever act as gametes, as in *Olpidium viciae.* All are apparently capable of accomplishing infection. On coming in contact with the host the swarmspore rounds up, effects penetration, and comes to lie within the host cell, where, for a brief period at least, it exists as a naked protoplast. It gradually

increases in size at the expense of the host protoplasm and during the period of vegetative growth is termed the thallus. At maturity it possesses a membrane and functions as a sporangium, freeing swarmspores which pass to the outside of the host through a more or less elongate **exit tube.** When two or more swarmspores enter the same host cell the resultant thalli sometimes copulate. Though the details of the sexual process in such cases are not well known and may differ in different species, there always exists in later stages a larger thallus united with one or more smaller thalli by open pore connections. The whole content of the smaller cell or cells enters the larger cell, and it then assumes a thick wall and matures into the resting spore. Presumably, therefore, the larger cell is female and the smaller cells are male. At least in some species (*e.g.*, *Olpidiopsis vexans*) it is known (Barrett 1912) that both the male and female cells have become plurinucleate, through division of the primary swarmspore nuclei, before the male cells have discharged their contents into the female. Whether at the moment of their initial contact the copulating cells are already provided with thin membranes is not certainly known, but seems likely. If they were then still naked protoplasts their complete merging to form a fusion cell, as in *Monochytrium*, would probably occur. The very early stages in the process are unknown. Though the copulating cells differ in size from an early period, it is possible that at the beginning of their association they are morphologically equivalent. When the male nuclei enter the female cell they appear to fuse in pairs with the female nuclei. The female cell finally assumes a thick wall, and is transformed directly into the resting spore. The use of the term oospore or zygospore in such cases results only in indefiniteness. The sexual process is clearly neither typically oomycetous nor typically zygomycetous. In the Ancylistales other intermediate types occur, and, though that group as a whole is placed by some students in the Oomycetes, zygomycetous tendencies in some of the genera at least (*e.g.*, *Ancylistes*) are seen in the absence of the oosphere and the direct copulation of the gametangia. In this order copulation is effected in some cases by means of a conjugation tube. In *Zygorhizidium willei* and *Polyphagus euglenae* of the Chytridiales uninucleate thalli copulate in similar fashion by means of a conjugation tube. The individual putting out the tube is usually considered to be from that fact alone clearly the male. It is of

interest, nevertheless, to note that the resting spore in *Polyphagus* is formed in the tube rather than in the so called female individual.

A consideration of these variations in the sexual process as exhibited in the lower Phycomycetes indicates clearly that various primitive types of sexuality exist here which are, strictly speaking, neither oomycetous nor zygomycetous. Some of these probably represent lateral lines of development or terminations of series having little if any connection with the two main lines ending in the higher Oomycetes and Zygomycetes. Until these lower forms have been studied much more thoroughly the solution of the problem of their interrelationships cannot be reached.

In numerous genera of the Phycomycetes, species have been described in which a sexual stage is not as yet known to occur. In primitive members of the group, such as the lower Chytridiales, it is possible that some of these are forms in which sexuality has not yet arisen. In the higher Phycomycetes absence of a known sexual stage may be due to the existence in the species of a **heterothallic** condition, *i.e.*, segregation of sex in such a fashion that constantly some thalli are wholly male while others are wholly female. In such heterothallic species the presence of both sorts of thalli, and in most cases their actual contact, is necessary before a sexual union can be effected. It is possible that in some species one of the two sorts of thalli has died out completely, leaving the species unisexual. When both sexes occur in the same thallus the species is termed **homothallic.** Failure of a homothallic species to form sexual spores is usually attributed to unfavorable features of nutrition or other environmental factors. These factors are as yet only imperfectly understood.

The gametangia of the Phycomycetes are usually functional However, in several families (*e.g.*, Saprolegniaceae, Mucoraceae, Entomophthoraceae) sexual organs of normal aspect may fail to react sexually. In these cases spores morphologically equivalent to the sexual spores are formed **parthenogenetically.** In the Zygomycetes such spores have long been termed **azygospores.** In the Oomycetes they may well be called **aboospores.** They are capable of germination and the production of normal thalli. Though the chromosome condition in such cases has not been compared with that in normally sexual species it is probably unchanged throughout the entire life cycle. Since the fusion

nucleus of the mature oosphere is normally the only nucleus with the double chromosome number it is usual to regard the oospore as **sporophytic,** and since the fusion nucleus is thought to undergo immediate reduction in all members of the group the remainder of the cycle is termed **gametophytic.** Consequently forms which mature the oospore without fertilization are regarded as **apogamous.** Oomycetes in which oospores form in the complete absence of the antheridium are termed **apandrous.**

Classification.—The taxonomic study of the fungi has engaged the attention of mycologists for two hundred years. During this period various systems of classification have been proposed. Early students were content with any orderly arrangement of genera which placed together fungi of similar morphology. Modern workers have sought to provide a natural scheme of classification representing phylogenetic relationships.

At the beginning of this chapter, it has been shown that two outstanding points of view exist with respect to the origin of the fungi. Some students regard the group as monophyletic. Others look upon it as merely an assemblage of relatively unrelated forms, which have degenerated along several different lines from the algae. Until general agreement is reached as to the origin of the group, it is evident that no one system of classification will receive the unqualified endorsement of all authorities. It is true, also, that even an admittedly excellent classification has only temporary value. Investigation is constantly bringing to light new facts, and these at times change points of view and necessitate alteration in the content of groups and in their arrangement. It is not likely that any classification will ever be accepted as permanent.

The Phycomycetes are usually treated as a unit, and constitute the lowest of the three primary subdivisions (classes) into which the fungi are customarily divided. The number and content of the orders and families making up the Phycomycetes do not differ greatly in the various well known modern separations, but no two classifications are wholly alike. No one of them has been accepted generally as the standard. The best known treatments are those of Schröter (1892–1893) and Fischer (1892) published at practically the same time nearly forty years ago. Though now much out of date, they are still used by many students. In the classification of Schröter the Phycomycetes are separated into two sub-classes, (1) the Oomycetes, embracing

the orders Chytridineae, Ancylistineae, Monoblepharidineae, Saprolegnineae, and Peronosporineae, and (2) the Zygomycetes, including the Mucorineae and Entomophthorineae. Fischer recognizes three primary subdivisions, Archimycetes, Oomycetes, and Zygomycetes. In the Archimycetes he includes the genera incorporated by Schröter in the Chytridineae and Ancylistineae. In erecting this group he emphasizes the fact that in these forms mycelium is absent or poorly developed and sexual reproduction uncommon. In both classifications, the separation of the Oomycetes and Zygomycetes is based on the essential difference in the sexual process, oospores being characteristic of the former and zygospores of the latter. The two classifications differ further in several minor respects. The Pythiaceae, included in the Saprolegnineae by Schröter, are incorporated in the Peronosporineae by Fischer, and the Monoblepharidineae of Schröter are treated as a family of the Saprolegnineae by Fischer. Generic limits in the two separations are not in all cases identical, as will be emphasized in later pages.

In recent years, two other taxonomic treatments of the Phycomycetes have appeared, which are sufficiently outstanding to require special consideration. These have been presented by von Minden (1911) and Gäumann (1926). The classification of von Minden is intermediate in several respects between the separations of Schröter and Fischer. While he does not recognize the group Archimycetes, and his ordinal separations correspond essentially with those of Schröter, he includes the Pythiaceae in the Peronosporineae and in numerous other details follows Fischer. His paper as a whole is the most modern of the taxonomic treatments providing keys to families and genera. Gäumann concerns himself chiefly with problems of comparative morphology, and does not attempt a complete taxonomic separation. He removes the Olpidiaceae, Synchytriaceae, Plasmodiophoraceae, and Woroninaceae from the Phycomycetes and treats them as a lower group to which he applies the name Archimycetes. The Rhizidiaceae, Hyphochytriaceae, and Cladochytriaceae comprise the Chytridiales in his arrangement. He divides the Phycomycetes into Chytridiales, Oomycetes, and Zygomycetes. The Oomycetes include the Monoblepharidaceae, Blastocladiaceae, Ancylistaceae, Saprolegniaceae, Leptomitaceae, and Peronosporaceae. The Zygomycetes include the Mucoraceae, Endogonaceae, and Entomophthoraceae. The

recently published book by Gäumann and Dodge (1928) is a translation of this work of Gäumann. No attempt will be made at this point to criticize or explain the various pronounced changes advocated by Gäumann. In some cases this is done on the pages which follow in connection with the groups concerned.

In presenting the ordinal and family separations which appear in the present work the writer has tried to maintain a conservative point of view. Changes from the older established arrangements have been made only when they were clearly unavoidable. In such cases adequate explanations have been given. The inclusion of the Plasmodiophoraceae in the Chytridiales and the recognition of the order Blastocladiales constitute instances of this sort. On the whole the classification does not depart far from the older established points of view. The terminations *-ales* and *-aceae* for ordinal and family names respectively are those recommended by the International Rules of Botanical Nomenclature (Briquet 1912). They are now generally used in the taxonomic literature.

Though the eight orders into which the Phycomycetes are separated in the following key constitute rather definitely delimited groups, they tend to merge somewhat at their border lines. This is to be expected in any natural system. If the sum total of the characters of each group be taken into consideration the lines of separation will appear more sharp.

Key to Orders of Phycomycetes

I. Mycelium wholly absent in several families, in others present but poorly developed or evanescent; thallus at maturity functioning in large part or in its entirety in reproduction; sexual reproduction often unknown, when present of various kinds but not typically oomycetous or zygomycetous.

A. Thallus in most forms functioning essentially in its entirety in one capacity, at maturity usually acting as a single sporangium or gametangium or by cleavage becoming a sorus of like sporangia; resting spore not lying free in the gametangium.

1. **Chytridiales**, p. 43

B. Thallus at maturity divided by transverse septa into a chain of cells capable of functioning in various capacities, *i.e.*, as sporangia, male or female gametangia, or specialized vegetative cells; resting spore lying free in the female gametangium and resembling the oospore of higher orders; an oosphere apparently lacking.

2. **Ancylistales**, p. 117

II. Mycelium well developed, not evanescent; thallus at maturity functioning in relatively small part in reproduction; specialized cells cut off by

septa to function as reproductive organs; the remainder of the thallus retaining its vegetative character; sexual reproduction usually present; resting spores, identical in aspect with the sexual spores, developed in some genera parthenogenetically.

A. Male and female gametangia freeing ciliate gametes which fuse to form zygotes; zygote developing directly into the new plant without first becoming a resting spore; characteristic thick-walled chlamydospores formed asexually.

3. **Blastocladiales, p. 130**

B. Female gametangium not forming ciliate gametes; sexual fusion resulting in a thick-walled resting spore.

1. Contents of female gametangium differentiated at maturity to form one or more naked protoplasmic spheres termed oospheres; sexual identity of male and female gametangia evident; female gametangium (oogonium) larger and stouter than the male gametangium (antheridium); true gametangial copulation lacking; fertilization accomplished by passage of one or more male nuclei directly into the oosphere; oosphere maturing into a thick-walled oospore lying free in the oogonium; swarmspores formed in most genera. -**Oomycetes.**

a. Antheridium forming ciliate cells (antherozoids) which swim to the oogonium and fertilize the oosphere; fertilization tube lacking.

4. **Monoblepharidales, p. 138**

b. Antherozoids not formed; one or more male nuclei discharged into the oosphere through a fertilization tube put out by the antheridium.

(1) Forms typically aquatic and chiefly saprophytic; sporangia usually not deciduous, freeing endogenous spores; asexual cells functioning as conidia uncommon; oogonium forming one to many oospheres.

5 **Saprolegniales, p. 146**

(2) Forms typically terrestrial and parasitic, though species of aquatic, semiaquatic, and saprophytic habit occur; sporangia typically deciduous and wind disseminated, commonly termed conidia, in some cases freeing endogenous spores, in others germinating directly by germ tube; oogonium forming a single oosphere

6. **Peronosporales, p. 185**

2. Oospheres lacking; sexual identity of male and female gametangia not evident; the two cells usually indistinguishable in size and shape, and functioning alike; consequently the terms antheridium and oogonium not applicable; true gametangial copulation occurring and the merged protoplasts transformed into the zygospore; zygospore not lying

free; its wall formed directly from that of the gametangium; swarmspores absent in the group.—**Zygomycetes.**

a. Forms typically saprophytic; zygospores borne chiefly on aerial mycelium; asexual reproductive cells extremely various and representing steps in the evolution of the unicellular deciduous conidium from the many-spored persistent sporangium; conidia not shot away.

7. **Mucorales,** p. 234

b. Forms chiefly parasitic and entomogenous, a few forms saprophytic, a few others parasitic on plants; zygospores borne typically within the host; asexual reproduction almost always by conidia borne at the ends of specialized conidiophores and shot away at maturity

8. **Entomophthorales,** p. 281

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CHAPTER III

CHYTRIDIALES

The members of this order are characterized by extreme simplicity of form and structure, and are regarded as the lowest of all the fungi. They are commonly termed **chytrids.**

Mycelium is either wholly wanting or only slightly developed. When present it consists usually of delicate threads, the terminal branches of which taper to sharp-pointed, almost invisible tips. In only a few genera are the threads of broad diameter and definitely cylindrical as in most higher fungi. Frequently, the thallus is so limited in extent that its branches are confined to a single host cell. It is then said to be **monophagus.** In other cases, the branches enter several or many host cells, the term **polyphagus** being applied. In species in which mycelium is wholly absent the thallus functions in its entirety at maturity in reproduction. A single thallus may be transformed into a sporangium, a group (**sorus**) of sporangia, a resting spore, or a group (sorus) of resting spores. Two thalli may conjugate, one functioning as the male cell, the other as the female. In species possessing mycelium the reproductive cells are far more prominent than the vegetative threads.

The thallus, in the chytrids, has its beginning in almost all cases as a motile spore, **zoospore,** which comes to rest, enlarges, and finally attains the form and size characteristic of the mature thallus. Zoospores are amoeboid or ciliate. In the latter case, they are often called **swarmspores.**

In asexual reproduction zoospores are borne in indefinite number in a unicellular sac, called the **sporangium,** which may or may not, as indicated above, compose the entire thallus. During the summer in temperate regions several generations of the organism usually follow one another rapidly as long as a food supply is available. The sporangia produced at this period are typically thin-walled and may be termed **summer sporangia, thin-walled sporangia, swarmsporangia** or merely sporangia. Especially at the close of the season or in periods

of unfavorable environment they may be thick-walled, and are then termed **resting sporangia or resting spores.** When evidence is given that a sexual fusion accompanies their formation the terms **oosporangium, oospore, zygosporangium** or **zygospore** are often applied.

When, in parasitic species, the summer sporangia or resting spores are formed within the host cell they are termed **endobiotic** (**endophytic** when the host is a plant, **endozoic** when it is an animal). When they stand on the surface of the host, with only the nutritive hyphae penetrating into its interior, they are said to be **epibiotic (epiphytic** or **epizoic).** In saprophytic species they are either **intramatrical** or **extramatrical** depending on whether they lie in or outside of the matrix or substratum.

The summer sporangium is usually more or less globose or ovoid, though in some genera it is considerably elongated. At maturity its contents form one to many zoospores. These are usually ciliate and escape from the sporangium through a definite pore, which often terminates an elongate **exit tube.** More rarely the zoospores are non-ciliate and amoeboid. Occasionally, zoospores encyst in the sporangium and germinate by tubes *in situ.* In some genera the protoplast passes from the sporangium into an extruded thin-walled vesicle, which later bursts freeing the zoospores. In such cases the zoospores may or may not be completely delimited before passing into the vesicle. Since the vesicle functions as a sporangium, it is so called by many writers, while the initial cell, from which it arises, is termed the **prosporangium.**

When the mature thallus divides to form a group of sporangia or resting spores the group is termed a **sorus.** In some genera the entire protoplast flows from the thallus into a thin-walled vesicle and there divides to form the sorus. In such cases the initial thallus cell is called the **prosorus.**

The **resting spore** corresponds essentially in its methods of germination to the summer sporangium except that in some cases it functions as a prosorus and emits a vesicle in which a sorus of sporangia are formed. It is thicker walled than the summer sporangium and, though sometimes smooth, is often characteristically roughened, being tuberculate, echinulate, or reticulate.

In this order the zoospores are usually ciliate, and swim actively for a time before coming to rest and retracting their cilia. In most genera the zoospore, on becoming quiescent,

envelops itself in a thin membrane and is then said to be encysted. Some writers term it a **cystospore.** In the Plasmodiophoraceae and Synchytriaceae a membrane is not formed, and in these groups, composed wholly of parasites, the zoospore is capable of passing directly through the host cell wall into the cell cavity. In the other families the zoospore assumes a membrane, and germination is accomplished by the passage of the protoplast through a short exit tube or germ tube. In parasitic species this exit tube functions as an infection thread and penetrates the host cell wall. In the Olpidiaceae and Woroninaceae the protoplast of the cystospore then passes through the tube into the host and there develops into the mature thallus. In the typical epibiotic species (Rhizidiaceae) the germ tube of the cystospore acts as a holdfast and often develops into a system of delicate endobiotic rhizoids, while the spore itself enlarges and forms an epibiotic sporangium or resting spore. In the Cladochytriaceae epibiotic sporangia are sometimes formed in this way, but more often the protoplast of the swarmspore passes through the germ tube into the host and develops there into an extensive mycelium. Endobiotic sporangia and resting spores then develop from intercalary or terminal enlargements of this mycelium.

Sexual reproduction probably takes place in many of the genera of the order, but its presence has been satisfactorily demonstrated in relatively few species. Probably, subsequent investigations will show that the resting spores throughout the group are in most cases at least sexually produced. They are commonly termed resting spores, rather than oospores or zygospores, because the method of their formation is usually in doubt. Even in cases in which the details of the sexual process are completely known the terms oospore and zygospore are avoided since in these primitive forms sexuality is often intermediate in type between typical oomycetous and typical zygomycetous reproduction. Considerable variation in the sexual process is evident in the group, the general situation having been summarized in the preceding chapter (p. 34). The resting spore in some species (*e.g.*, *Olpidium viciae* and *Synchytrium endobioticum*) results from planogamic fusion of ciliate isogametes. In other cases (*Monochytrium*) gametes fuse in the amoeboid condition. Probably many species form their resting spores in this manner, the fusions not yet having been observed due to the difficulty of following the activities of such small motile

cells. In all such cases, summer sporangia result from zoospores and resting spores from zygotes. In other species, young thalli copulate (*e.g.*, *Olpidiopsis spp.* and *Pseudolpidiopsis spp.*) and a pore connection is formed between them. One cell then functions as the female and, after receiving the contents of the male cell, enlarges and is transformed by the thickening of its wall directly into the resting spore. The spore does not lie free in the oogonium as in the Oomycetes. The emptied male cell remains attached to the spore even at maturity and was termed the companion cell by earlier mycologists who failed to appreciate its real character. In some cases, several male cells conjugate with a single female cell, and the resting spore bears consequently several companion cells. In *Zygorhizidium* a conjugation tube is put out by one individual and its contents are discharged through the tube into the other which then develops into the resting spore. In *Polyphagus* a similar tube is formed but the resting spore develops in the tube.

It is evident in the light of this great variation in the sexual process that the order Chytridiales can not be incorporated in the old superordinal group Oomycetes, as has been attempted by Schröter (1892: 63).

In the separation of the families of the order the treatment here adopted is not identical with that of any standard text. Except in the incorporation of the Plasmodiophoraceae, it agrees in the main with that of von Minden (1911: 226), though his recognition of the family Hyphochytriaceae is not followed. His monograph of the order is the most recent general treatment. We have not seen fit to follow Gäumann (1926: 15) in excluding from the Phycomycetes those lower families of the present order which do not form mycelium. His limitation of the term Archimycetes to such forms will prove confusing to all students who have applied it in the sense of Fischer to the Chytridiales and Ancylistales.

Below in the discussion of the Plasmodiophoraceae the reasons for the incorporation of this family in the Chytridiales are given. The point is stressed that the order as here recognized is clearly a polyphyletic group. The inclusion of an additional border line family is consequently the more easily justified. The results of future investigation will doubtless enable the student of phylogeny to arrange the members of the order in several natural lines, but at present this does not seem possible. Consideration

of the morphology of the zoospore will probably afford one of the more fundamental bases of separation, since this structure is presumably primitive. It is of interest to note in this connection that in the Woroninaceae alone is this cell biciliate as in the higher orders. The Chytridiales are of special interest to that group of students who believe that the higher fungi arose from the lower (Atkinson 1909 *b*). By other students they are regarded as degenerate unicellular green algae or degenerate Oomycetes. Although the writer is inclined to the belief that the fungi have arisen from unicellular non-chlorophyll bearing organisms and that the group is phylogenetically a unit, it seems evident that certain lines of development have progressed a relatively short distance. The terminations of several such lines apparently exist today in the Chytridiales, while one or more other lines may be assumed to have produced the higher forms.

The order Chytridiales embraces approximately two hundred known species. The majority were described first from Central Europe and may not have been encountered elsewhere. The group has been studied relatively little, and numerous undescribed species doubtless await the attention of the investigator in all parts of the world. Many are probably cosmopolitan. Most of the known species are true parasites in plants or animals. Of those in plants fully half occur in fresh-water algae, almost as many live in higher plants, while the remainder occur in marine algae, aquatic fungi, and in pollen grains, rust spores, and other similar bodies which fall into the water. A few species are parasitic in Protozoa, and some are saprophytic in submerged, decaying plant or animal remains. All the species are microscopic, though in some cases their presence stimulates the host to form noticeable galls, swellings or discolorations. In the treatment which follows, the effort is made to include all known genera. The miscellaneous character of the literature, has made this difficult, however, and it is to be expected that some forms have been overlooked.

Key to Families of Chytridiales

I. Mycelium wholly lacking; thallus always intramatrical.
   A. Thallus existing, through early stages at least, as a naked, more or less amoeboid protoplast, often somewhat obscured by the protoplasm of the host cell, finally (in most cases) fragmenting

into a number of naked protoplasts, each of which then assumes a wall and functions as a summer sporangium or resting spore.

1. Thallus never functioning in its entirety as a single sporangium or resting spore, but in some cases said to form a soral membrane before breaking up into sporangia; sporangia germinating by a small number (one to eight) of amoeboid or uniciliate zoospores; cilium demonstrated in but few cases, where known attached to the anterior end of the zoospore; vegetative mitosis of a peculiar protomitotic or cruciform type.

   1. **Plasmodiophoraceae**, p. 48

2. Mature thallus in some genera forming a membrane and functioning as a single sporangium or resting spore, in others fragmenting into a number of naked protoplasts each of which then assumes a membrane; a common soral membrane never formed; sporangia typically multispored; zoospores laterally biciliate.

   2. **Woroninaceae**, p. 66

B. Thallus provided from an early period with a thin membrane, clearly discernible within the plasma of the host cell; zoospores uniciliate; cilium attached at the posterior end of the spore.

1. Thallus at maturity functioning in its entirety as a single sporangium or resting spore.

   3. **Olpidiaceae**, p. 71

2. Thallus at maturity either developing a thick wall and functioning as a resting spore, or its protoplast divided by cleavage planes to form a sorus of sporangia enclosed in a common soral membrane.

   4. **Synchytriaceae**, p. 80

II. Mycelium present, though usually only slightly developed and of delicate threads of small diameter; thallus intra- or extramatrical.

A. Mycelium not wide-spreading, usually confined to one or two cells of the host, bearing only a single sporangium, and usually in open connection with it at maturity; sporangia usually epibiotic.

   5. **Rhizidiaceae**, p. 88

B. Mycelium wide-spreading, developing terminal and intercalary enlargements which are transformed wholly or in part into sporangia or resting spores.

   6. **Cladochytriaceae**, p. 100

Plasmodiophoraceae

Inasmuch as the members of this family have long been regarded by many students as parasitic slime moulds their inclusion in the Chytridiales necessitates a more lengthy explanation that would otherwise be given. It can best be provided by

a presentation in sequence of the essential historical facts concerning the group.

The oldest genus recognized at present as a member of the family is *Plasmodiophora*. It was founded by Woronin (1878) on the causal organism of clubroot of cabbage, *P. brassicae* Wor. In his discussion of the genus, Woronin indicates clearly that he regarded the organism as an undoubted relative of the Myxomycetes. Incidentally, he concluded that the legume tubercle organism, long known and variously classified, should be placed near it. Other students of the fungi accepted his point of view, and a search for additional "parasitic slime moulds" followed. Several new species were added to *Plasmodiophora*, and two new monotypic genera *Tetramyxa* and *Sorosphaera* were erected. The legume tubercle organism which had already received a number of names (*Schinzia leguminosarum* Frank, *Bacillus radicicola* Beijerinck, *Rhizobium leguminosarum* Laurent, *Bactridium radicicola* Fischer) was now redescribed as *Phytomyxa leguminosarum* by Schröter (1886:134), and a new order, *Phytomyxini*, was erected for its reception. Because the group (as Phytomyxinae) was incorporated later by Schröter in the standard work, Engler und Prantl's, Die Natürliche Pflanzenfamilien, it was generally accepted. It includes there the four genera *Plasmodiophora*, *Phytomyxa*, *Tetramyxa*, and *Sorosphaera*, represented at that time by seven species, *Pl. brassicae* Wor., *Pl. alni* (Wor.) Möll., *Pl. elaeagni* Schröter, *Phy. leguminosarum* (Frank) Schröter, *Phy. lupini* Schröter, *T. parasitica* Göbel, and *S. veronicae* Schröter.

Later, the legume tubercle organism was proved to be beyond question one of the bacteria, and more recent investigations indicate that the root tubercles on *Alnus*, *Elaeagnus*, *Myrica*, and certain other non-leguminous plants are caused by the same species or closely related ones. Consequently, *Plasmodiophora alni* and *Pl. elaeagni* have disappeared from the Phytomyxinae along with *Phytomyxa*. In a review of this situation, Maire and Tison (1909) point out that, since *Phytomyxa* has been removed, the name Phytomyxinae is no longer appropriate. They use instead Plasmodiophoraceae, and under this heading list the three remaining genera. They follow Schröter in separating them on the basis of the arrangement of the spores, *i.e.*, *Plasmodiophora* (spores free from one another), *Tetramyxa* (spores clinging together in tetrads), *Sorosphaera* (spores arranged to

form a hollow sphere). In a later and more extensive paper they (Maire and Tison, 1911) erect two new genera, *Molliardia* and *Ligniera*, and present a somewhat revised classification in which they stress as of primary significance the question of whether a given organism results in hypertrophy of the host.

Although the genus *Spongospora* Brunchorst (1887), now regarded as a member of the group, was described relatively early, its existence was overlooked or ignored by all of these later writers. It was demonstrated to be an undoubted member of the group by Osborn (1911 *a*) at about the time that Maire and Tison published their second paper. Subsequently, several additional genera have been described by other authors. These are all discussed below and in spite of fragmentary data in the case of some species, the attempt is made to present a complete picture of the family as it exists today.

The writer is not the first to incorporate the Plasmodiophoraceae in the fungi. Gäumann (1926) and Gäumann and Dodge (1928) incorporate the group in the Archimycetes, and emphasis has been placed by various investigators on facts which seemed to them to justify the inclusion of the group in the fungi. There has been considerable diversity of opinion expressed in recent years, however, as to the relationships of the group. Pavillard (1910) concludes that these forms are a branch of the Myxomycetes in which modifications have resulted from the parasitic habit. Schwartz (1914), while admitting that they are related to the Myxomycetes, regards the differences as so great that he treats them as intermediate between this group and the Chytridiales. Maire and Tison (1911) feel that they have originated from the Chytridiales, while Cook (1926) thinks that they show relationship with the Protozoa.

Students of the cytology of these forms have been impressed by the great similarity which the various genera and species show in the aspects of their nuclear behavior, and by the fact that they differ from other groups in exhibiting in their life cycle two entirely different types of nuclear division. One type occurs throughout the growth of the thallus or myxamoeba; the other immediately precedes spore formation or zoospore delimitation, and consists of two successive divisions which are believed to constitute reduction. The nuclear division which occurs during the growth period and which may be termed somatic has been commonly termed the "cruciform division" or protomitosis.

Nothing identical with this type of division has been seen in any other group of organisms, though in some of the most primitive Protozoa (order Lobosa) it is said to be approximated. Several workers have justified their inclusion of doubtful species in the Plasmodiophoraceae on the single point of their possession of this type of division. Before the two reducing divisions occur a stage exists in the cycle in which the stainable chromatin of each nucleus is extruded into the cytoplasm. This is termed the **"akaryote"** stage. The two mitoses which immediately follow are typical, and result in a tetrad of nuclei. According to Cook (1928 *b*) these nuclei become in some cases the centers of spores, while in others the primary nucleus of the spore is diploid and reduction occurs in zoospore formation. During the cruciform division the nucleolus divides and persists in the daughter nuclei. Since the dividing nucleolus is drawn out into a dumb-bell shape, and lies at right angles to the chromatin gathered at the equatorial plate, the division figure as viewed from the side has the aspect of a cross. The essential feature of this mitosis is thus the persistence and division of the nucleolus. In the reduction divisions the nucleolus disappears, as in most higher plants, and is re-formed *de nova* in the daughter nuclei. A nuclear fusion (**karyogamy**) may occur at some point in the cycle, but, though reported in one or two cases, cannot be said to have been satisfactorily demonstrated. Several workers have expressed the opinion that it will be found in the pairing of zoospore-like gametes when germinations are obtained in satisfactory quantity. The whole nuclear situation is well summarized in the recent papers of Cook (1926; 1928 *b*) on *Ligniera*. Just how much significance should be attached to the cruciform division is perhaps in question, and conclusions concerning the taxonomic position of the group based on this feature alone would seem premature in the light of our ignorance of nuclear division in various lower groups. The spores have been observed to germinate in but few species of the family and by but few investigators. In *Plasmodiophora*, according to Woronin (1878) and Chupp (1917) the spore wall cracks open and the protoplast emerges as a single zoospore which swims for a time with a single cilium attached at the forward end. The posterior end of the zoospore is figured by Woronin as amoeboid. If the zoospores could be shown to be of this type throughout the group, a character indicating relationship of this family

and the Myxomycetes would be provided, but the data concerning germination are so few and contradictory that conclusions may not yet be safely drawn. In *Plasmodiophora* the amoeboid character described by Woronin was not observed by Chupp (1917). In *Spongospora* according to Johnson (1908) eight zoospores are freed from the spore, while Kunkel (1915) describes but one. In *Ligniera* the number varies, according to Cook (1928 *b*), from four to eight. The assumption that the zoospore penetrates the host directly without first encysting on the surface in an enveloping membrane also requires verification. If true it may perhaps be regarded as evidence of relationship with the Synchytriaceae.

In the host the earliest stages observed show these parasites (except in *Spongospora* according to Kunkel) as intracellular, uninucleate, amoeboid protoplasts, and it may be assumed in most cases at least that they penetrate in this form. In the host cell the protoplast (**myxamoeba**) becomes multinucleate, increases in size, and absorbs nutriment from the host. It may or may not fragment into daughter myxamoebae. At maturity each myxamoeba is split by cleavage planes into uninucleate bits, each of which envelops itself in a wall and assumes a more or less spherical form. These bodies have been termed spores by all workers in the group. After passing through a period of rest, however, they germinate by one or more swarmspores or myxamoebae, and seem to be comparable in many respects to the resting sporangia of other families of the Chytridiales. The same is true also of the so called spores of the Myxomycetes. These "spores" (resting sporangia) may remain attached to one another forming groups of definite form, or they may fall apart and lie free in the host cell.

The mature multinucleate myxamoeba which fragments to form these spores apparently remains naked in most cases, so that the spores are not enveloped in a common soral membrane; but Schwartz states clearly that such a membrane is formed in *Sorosphaera*. The papers of Borzi (1884: 6) and Němec (1911 *a*; 1913 *a*) on *Rhizomyxa*, *Sorolpidium*, and *Anisomyxa* lend support to the assumption that both types of development exist in the group. If this is true the group in this respect is intermediate between the Myxomycetes and the Synchytriaceae.

The peculiar phenomenon of elimination which in the Myxogastres results in the formation of capillitium threads and "sporangial" walls is wholly lacking in the Plasmodiophoraceae.

When several myxamoebae exist together in the same host cell, and continue to grow, it might be expected that they will finally come into actual contact, and being naked fuse. They have been stated to do so in some species, and certain writers have termed the apparently united and homogeneous mass, which tends to fill the host cell, the plasmodium. Other investigators deny that fusion is complete, and maintain that mitosis is simultaneous only in a given myxamoeba, not throughout the entire host cell. In *Spongospora* according to Kunkel (1915: 273) the uninucleate myxamoebae which escape from the various spores composing a spore ball may lie in such close contact that "they seem to fuse and cannot be distinguished as separate bodies." He states further that such "baby plasmodia" may come together to form larger ones, and that infection of the host is effected by the penetration of the multinucleate "plasmodium" between the cells of the tuber. In the Myxogastres where the term **plasmodium** was first used by Cienkowski an as yet unexplained phenomenon of mutual attraction exists between the motile cells. They are drawn together, and multiple cell fusions result in the formation of an enlarging naked amoeboid protoplast. This body is termed a plasmodium not merely because it is naked and multinucleate, but more essentially because it is formed by multiple fusion of uninucleate motile cells which are drawn together by mutual attraction. To the writer it does not seem that such a true plasmodium has been found in any of the Plasmodiophoraceae. In those species of the family in which a fusion is conceded by all workers to be lacking, and in which the nuclei of the mature multinucleate myxamoeba clearly arise through repeated division from the nucleus of the infecting zoospore, the use of the term plasmodium seems wholly unjustified.

In attempting to indicate the bases on which it seems desirable to incorporate the Plasmodiophoraceae in the fungi rather than in the Myxomycetes it is necessary to deal in generalizations on account of inadequate data. Enough is known concerning the group, nevertheless, to warrant the attempt. In the character of the zoospore and in the unusual type of vegetative mitosis the Plasmodiophoraceae are unlike other known fungi. The zoospore seems to resemble that of the Myxogastres, the nuclear division to some extent that of certain Protozoa. In the absence of capillitium and so called "sporangial" walls, in the absence of a true plasmodium, and in the presence of para-

sitism the group differs strikingly from the Myxogastres and corresponds with the Woroninaceae and Synchytriaceae of the Chytridiales. In the small and apparently rather definite number (1–8) of zoospores freed in the germination of the sporangium ("spore") the Plasmodiophoraceae resemble the Myxogastres more than they do the Woroninaceae and Synchytriaceae where the number is usually much larger. Ignorance of the facts concerning the position of nuclear fusion and reduction division in the cycle of the various groups, and conflicting evidence concerning the presence or absence of a soral membrane render these characters of little value for purposes of contrast.

In summarizing the available facts it would seem that the Plasmodiophoraceae resemble the Myxogastres less than they do the Woroninaceae and Synchytriaceae. Their failure to form a true plasmodium is regarded in this connection as an essential feature. However, in placing the family in the Chytridiales, it should not be assumed that the relationship to members of this order is necessarily close. It has been pointed out above in the ordinal diagnosis that the Chytridiales constitute a large assemblage of forms which seem to have been derived along a number of different lines. A correctly drawn phylogenetic tree would probably completely disrupt the group. These forms have been treated together in one order merely because they constitute the most primitive fungi, not because they are regarded as a coherent group of closely related genera. A more natural arrangement is much to be desired, but cannot as yet be attempted. This situation makes much easier the inclusion of the Plasmodiophoraceae in the group, and taking into consideration the striking difference in the morphology of the swarmspore in the three families it does not seem unreasonable to assume that the Woroninaceae and Synchytriaceae are as closely related to the Plasmodiophoraceae as to each other. To the writer it seems likely that these several groups have arisen more or less in parallel from yet more primitive Protozoa, and wholly independent of the Myxogastres which have arisen from the same or different Protozoa along another line. The existence in a limited section of the Protozoa of a type of nuclear division resembling the cruciform division of the Plasmodiophoraceae indicates perhaps the origin of this family, but does not of necessity preclude the possibility that other families, which now possess a higher type of mitosis, have arisen from the same or a closely

related group. In an interesting discussion of the "interrelationships of the Protista and the primitive fungi" Cavers (1915: 168) expresses a similar point of view but recognizes the Plasmodiophorales as a separate group, preferring not to include them in either the Myxomycetes or Chytridiales. The student will find in his article a wealth of information concerning the Protozoa which is not available in the general mycological literature.

Key to Genera of Plasmodiophoraceae

I. Spores at maturity not united; lying free in the host cell.
1. **Plasmodiophora**, p. 55

II. Spores at maturity remaining attached to one another in some definite type of aggregation.
A. Spores clinging together in tetrads or dyads.
2. **Tetramyxa**, p. 59

B. Spores united in larger numbers to form more or less definite spore balls.
1. Spore balls typically spherical to ellipsoidal, and hollow, consisting of a peripheral layer of spores enclosing a central cavity.
3. **Sorosphaera**, p. 60

2. Spore balls in the form of flat two-layered plates with a central cavity small or lacking.
4. **Sorodiscus**, p. 63

3. Spore balls sponge-like, essentially solid, lacking a central cavity but traversed by prominent fissures.
5. **Spongospora**, p. 64

1. **Plasmodiophora** Woronin (1878).

The genus *Plasmodiophora* was founded by Woronin on the single species *Pl. brassicae* Wor., which he had shown to be the cause of clubroot of cabbage and other cruciferous plants (Fig. 1). Subsequently a considerable number of imperfectly known organisms have been placed in this genus by various writers, but no one of them can be retained in it with assurance. It seems best for the present to regard the genus as monotypic, and to base the discussion on the classical paper of Woronin and on the results of certain more recent investigations on *Pl. brassicae.*

The disease caused by this species is well known on cabbage, and occurs less commonly on turnip, cauliflower, rutabaga, Brussels sprouts, and other similar cultivated and wild hosts. It results in pronounced malformation of the roots, and has

FIG. 1.—*Plasmodiophora brassicae* Woronin. A young cabbage plant showing typical malformation of roots. (*After Chupp 1917.*)

received in consequence various common names such as clubroot, and fingers and toes. The diseased roots are usually greatly enlarged locally, the swellings or galls varying in size and shape. On cabbage especially they are typically large and fusiform.

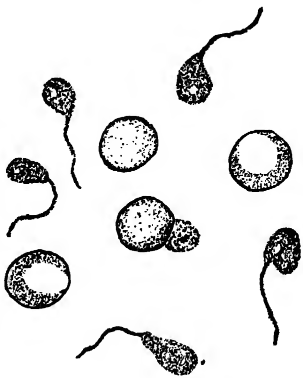

FIG. 2.—*Plasmodiophora brassicae* Woronin. Spores and swarmspores. (*After Chupp 1917; fig. 97.*)

The organism gains entrance into the roots from the soil through root hairs or other epidermal cells. Inoculation experiments performed by Kunkel (1918: *pl. 61*) show that infection may occur also through the epidermal cells of the stem below ground. The organism enters as a uninucleate amoeboid zoospore (myxamoeba). In the host cell it increases in size, becomes multinucleate (Fig. 3, *a*), and fragments into a number of daughter myxamoebae (Fig. 3, *b*). When the host cell divides several of these myxamoebae are usually incorporated in each of the daughter cells. Other cell divisions follow and soon a group of infected cells exists. These little clusters of diseased

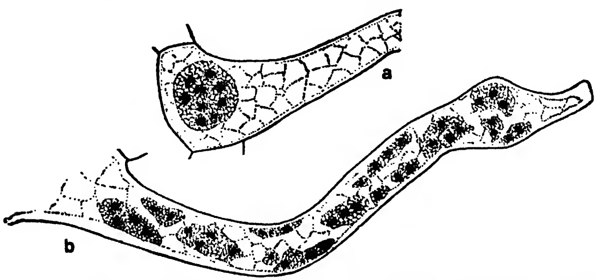

FIG. 3.—*Plasmodiophora brassicae* Woronin. (*a*) Multinucleate myxamoeba in base of root hair of cabbage. (*b*) Root hair containing a number of daughter myxamoebae resulting from division of the primary myxamoeba. (*After Chupp 1917; fig. 104.*)

cells resulting from primary infection by a single zoospore were termed by Woronin "*Krankheitsherde.*" Although Nawaschin (1899), who first used modern cytological methods in the study

of *Plasmodiophora*, states that the myxamoebae never migrate through the host cell walls into adjacent cells, later workers (Lutman, 1913: 3; Chupp, 1917: 435; Kunkel, 1918: 570) find that the organism spreads widely through the tissue by direct migration. Consequently, as Kunkel points out, many thousands of separate "*Krankheitsherde*" may result from a single primary infection. In fact, Kunkel states that the typical large club is the result of a single infection.

In the early stages of its intracellular existence the parasite does not interfere sufficiently with the functioning of the host cell to prevent its normal nuclear and cell division. Later,

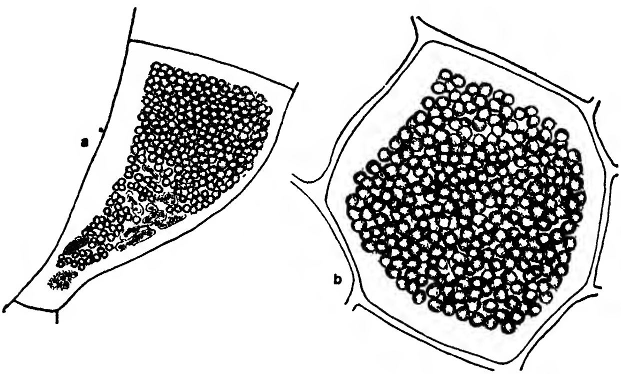

FIG. 4.—*Plasmodiophora brassicae* Woronin. (*a*) Formation of spores. (*b*) Mature spores (*After Chupp 1917, fig. 102.*)

the host protoplasm is largely absorbed, and the myxamoebae increase in size until they practically fill the cell. This brings them into direct contact and they are said by some workers to be completely merged. Others state that their identity is never lost, and that nuclear divisions are simultaneous only in a given myxamoeba, not throughout the whole mass. In any case, the host cell is finally almost or completely filled with the protoplasm of the parasite. The two nuclear divisions which are believed to constitute reduction occur, and the spores are cut out about the resultant nuclei (Fig. 4, *a*). They are more or less spherical and are provided with definite smooth membranes. Although the spores do not break apart simultaneously they lie

at maturity entirely free from one another and are not aggregated in any manner (Fig. 4, *b*). They are finally freed by the disorganization of the host tissue, and are disseminated in the soil water. Under favorable conditions each spore splits open and germinates by a single zoospore, which swims for a time (Chupp 1917: 425) with a single cilium attached to the forward end (Fig. 2). It finally comes to rest, and, having penetrated the host, exists in the cell in the non-ciliate amoeboid state. Woronin described the free-swimming spore as also amoeboid. Germination has been seen by few investigators and the accounts are contradictory (see *U. S. Dept. Agr. Tech. Bul.* 181, p. 7, 1930).

An unconvincing account of the life history of the organism, widely at variance with all previously published results, has been presented recently by Jones (1928: 313). He states that the spore in germination frees one to twenty ciliate cells and that these undergo a sexual fusion in pairs.

The genus has been used from the beginning as a dumping ground for doubtful species. It is pointed out above that *Pl. alni* and *Pl. elaeagni* were based on the legume tubercle organism or related species. Several species, *Pl. vitis*, *Pl. californica*, *Pl theae*, and *Pl. orchidis* are now known to have been founded merely on the products of cell disorganization. More recently *Pl. halophilae* Ferdinandsen & Winge (1913) has been described from the petioles of *Halophila ovalis;* a species has been described on sugar cane as *Pl. vascularum* Matz by Matz (1920) Bourne (1922) and Cook (1924; 1929); *Pl. tabaci* Jones (1926) has been discussed in connection with tobacco mosaic; and at least two other species, *Pl. ficus-repentis* Andreucci (1926) and *Pl. humuli* Nicholls (1924) have been published. In none of these cases has sufficient detail of life history, morphology, and cytology been provided to justify their inclusion in this genus as more than doubtful forms.

2. **Tetramyxa** Gobel (1884).

The genus was founded on the single species *T. parasitica* Gobel parasitic on *Ruppia rostellata,* a member of the pond weed family. The organism causes the formation of peculiar whitish galls on all parts of the plant except the roots. The genus is characterized by the tendency of the spores to cling together in tetrads. Sometimes they are found in dyads, or as single spores. More rarely large binucleate spores occur.

The host is infected by the uninucleate zoospore. This becomes multinucleate and divides, so that the host cell often contains several multinucleate myxamoebae. These grow and may come in contact but are never completely fused. Each myxamoeba forms its spores independently, and they may be in various stages of completion in the same host cell. Prior to spore formation the protoplasm of each myxamoeba segments into uninucleate spore mother cells. Two divisions, believed to constitute reduction, then occur, and the spore mother cell is cut by two perpendicular planes into four uninucleate cells, each of which assumes a cell wall and becomes a spore. These four spores tend to remain permanently united.

Molliard (1909) described a second species, *T. triglochinis* Molliard, on a parasite occurring on *Triglochin palustre*. Galls are formed on various parts of the plant above ground. The life history of this organism is imperfectly known. A multinucleate myxamoeba segments in the host cell into uninucleate portions and these after several nuclear divisions again segment. Tetrads of globose bodies, described by Molliard as spores, are thus formed. Maire and Tison (1911) state that these lack a definite cell wall and consequently are not comparable to the spores of other members of the group. These authors have seen fit, therefore, to erect a new genus *Molliardia* Maire & Tison for this species, which they retain in the Plasmodiophoraceae only provisionally. Until the species is better known it seems more logical to retain it in *Tetramyxa* as a doubtful form.

3. **Sorosphaera** Schröter (1886: 135).

As founded by Schröter the genus *Sorosphaera* included only one species, *S. veronicae* Schröt., occurring in Europe on various species of *Veronica*. It causes the formation of galls on various parts of the plant, leaves, petioles, stems, etc. After infection by the uninucleate, amoeboid zoospore the host cell becomes greatly enlarged. The parasite grows, becomes multinucleate, and divides, several multinucleate protoplasts thus coming to exist in the same host cell. By host cell division "*Krankheitsherde*" are formed as described for *Plasmodiophora*, but direct migration through the cell walls has not been observed. The several multinucleate protoplasts in a single host cell increase in size, but never fuse with one another. Although the nuclei of each myxamoeba divide simultaneously, the nuclei of adjacent

myxamoebae divide independently. Finally, the protoplasm splits up into uninucleate bits, and each of these rounds up, assumes a wall, and becomes a spore. The spores formed by each myxamoeba remain attached to one another, the whole being in the form of a hollow sphere, which, according to Schröter (1899) and Schwartz (1911) is enveloped in a very thin soral membrane. These spore balls are later freed by the disintegration of the host, and each spore germinates by a single zoospore.

Two other species, *S. junci* Schwartz (1910) and *S. graminis* Schwartz (1911), were later added to the genus. These forms correspond to *S. veronicae* Schröt. in all the essential features of the life cycle, though the spore balls are much less regular in form, the spores sometimes adhering merely in chains. The host is not stimulated to form galls, the attacked roots being even thinner than the normal ones. When Maire and Tison (1911) founded their new genus *Ligniera*, to include all the species of the family which do not cause hypertrophy of the host, they transferred to it *S. junci;* and the following year *S. graminis*, which had meanwhile been published, was placed in *Ligniera* by Winge (1912). Subsequently, Cook (1926) has shown by inoculation experiments that these two species are identical, and that several other species (*L. bellidis* Schwartz, *L. menthae* Schwartz, *L. alismatis* Schwartz, *L. pilorum* Fron & Gaillat) more recently described were also based on this one species. The genus *Ligniera* contains several other species (*L. radicalis* Maire & Tison, *L. verrucosa* Maire & Tison, *L. isoëtes* Palm). Cook (1926) considers it highly probable that *L. radicalis* is also identical with *S. junci*. On the other hand, *L. verrucosa* Maire & Tison is clearly a distinct species, marked by its roughened spores and their less evident tendency to cling together in definite masses; and *L. isoëtes* Palm, if in fact a member of this group, is certainly distinct.

As the genus *Ligniera* Maire & Tison was based merely on a host reaction the writer is wholly disinclined to accept it as valid. It is clear that two hosts may react quite differently to a given parasite, one being stimulated to gall formation, while the other is not. It seems best for the present to include all of the species in *Sorosphaera*, even though in some the tendency to form definite spore balls is much less evident than in the type species *S. veronicae* Schröter. The genus as thus reconstituted includes besides the type also *S. junci* Schwartz, and tentatively

as doubtful members *S. radicalis* (Maire & Tison), *S. verrucosa* (Maire & Tison), and *S. isoëtes* (Palm). Further study may result in the transfer of some of these latter forms to other genera.

A discussion of the doubtful genus *Rhizomyxa* Borzi (1884) may be inserted most logically perhaps at this point. This genus includes only the type species, *R. hypogaea* Borzi, described as parasitic in the roots of a number of flowering plants. It has been variously interpreted in the literature. Borzi pictured and discussed both a sexual and an asexual stage (Fig. 5),

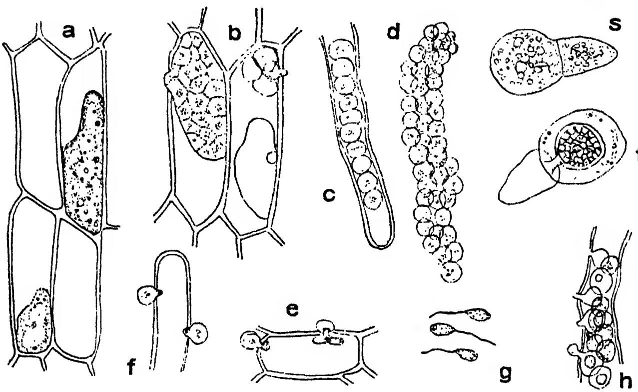

FIG. 5.—*Rhizomyxa hypogaea* Borzi. (*a*) Young thalli in cortical cells of *Stellaria media*. (*b*) Formation of sporangia. (*c*, *d*) Sori of sporangia, that at (*c*) in a root hair. (*e*, *f*) Zoospores infecting host cells. (*g*) Swarmspores. (*h*) Germinating sporangia with exit tubes. (*s*) Thallus divided by septum to form oogonium and antheridium. (*t*) After fertilization showing oospore in oogonium. (*After Borzi 1884.*)

but in the light of later work on other forms it seems highly probable that he based his description on a mixture of two or more different organisms. In the sexual process as described the thallus elongates and becomes septate into two unequal cells, one of which functions as an antheridium and the other as an oogonium. In the oogonium a differentiation of the contents into periplasm and ooplasm precedes fertilization, and at maturity a single oospore lies free in the oogonium. This account was accepted by Schröter (1892: 91) and he was led by it to place the genus in the Ancylistales. Fischer (1892: 69), von Minden (1911: 278), and others have excluded this stage from consideration. In the asexual phase, according to Borzi, the thallus is

at maturity a naked, multinucleate plasma which tends to fill the host cell. It may assume a membrane and function directly as a multispored sporangium, or it may break up while yet naked into a number of uninucleate bits each of which becomes invested in a wall. Each of these bits is comparable to the spore of *Sorosphaera* and on germination frees two to four zoospores. Maire and Tison regard *Rhizomyxa* as a complex of several organisms, and feel that this phase is probably merely *S. verrucosa*. The multispored sporangium may be that of an *Olpidium*.

More recently Němec has described two genera, *Sorolpidium* Němec (1911 *c*) and *Anisomyxa* Němec (1913 *a*), which should be given consideration in connection with *Rhizomyxa*. In the first, based on *S. betae* Němec, found in the living cortical cells of *Beta vulgaris*, the thallus persists to maturity as a naked multinucleate protoplast, and then is said to become invested in a thin membrane. Fragmentation finally results in the formation of a sorus of spores each of which later frees one to several zoospores. (See Guyot, A. L., *Rev. Path. Veg. et Ent. Agric.*, **14**: 176–183, 1927.)

In *Anisomyxa*, based on *A. plantaginis* Němec, found in the roots of *Plantago*, a similar situation exists. The individual sporangium may be relatively large, and frees a considerable number of spores. A common soral envelope was not observed. Němec's accounts do not carry conviction, and leave us in doubt concerning essential points in the life cycle in both genera. If he has not misunderstood his material these forms seem to be intermediate between *Plasmodiophora* and the Synchytriaceae. They should be studied further.

4. **Sorodiscus** Lagerheim & Winge (Winge, 1912).

In 1870, Kareltschikoff and Rosanoff described peculiar flat plate-like bodies which they found in the cells of *Callitriche autumnalis*. These bodies were later observed by Lagerheim in *C. vernalis*, and were recognized by him to be spore aggregations of one of the Plasmodiophoraceae. In 1912, Winge, working over Lagerheim's material, made these the basis of the new genus *Sorodiscus* and the new species *S. callitrichis* Lagerheim & Winge.

The spore aggregations are flattened plates of uniform thickness but of varying outline and diameter depending on the size and form of the host cell. The plate consists of two layers of

small polygonal cells, the spores. Between the two layers a small lumen occasionally occurs. This indicates that the plates are in reality much flattened hollow spheres or ellipsoids, and the genus is believed by Winge to be very close to *Sorosphaera.* Winge did not observe infection nor the uninucleate stage of the myxamoeba. Later stages were studied, and the form seems to correspond in the main to other members of the group. Young myxamoebae and mature spore balls were observed together in the same host cell. The individual spores are finally spherical. Spore germination was not observed.

5. **Spongospora** Brunchorst (1887).

The spore balls of *Spongospora* are, as the name signifies, tiny sponge-like aggregations of spores. The interior of the ball, unlike that of *Sorosphaera,* is essentially solid, and is traversed by broad fissures which open to the surface as prominent lacunae (Fig. 6). In shape the ball is globose or somewhat elongated, and the individual spores, while actually polyhedral from mutual pressure, are potentially spherical.

Fig. 6.—*Spongospora subterranea* (Wallroth) Lagerheim. A single spore ball. (*Original.*)

The genus contains the single species, *Spongospora subterranea* (Wallroth) Lagerheim, cause of powdery scab of potatoes. When Brunchorst erected the genus he named the organism *S. solani,* not realizing that the earlier name *Erysibe subterranea* Wallroth (1842) had been given to it. The identity of the two forms was recognized by Lagerheim (1892: 104), and the existence of other early synonyms was noted. Martius (1842: 28) named the species *Protomyces tuberum solani,* and Berkeley (1846: 33) called it *Tubercinia scabies.* The organism came into prominence through the papers of Massee (1908) and Johnson (1907; 1908; 1909) on economic aspects of the potato disease. Massee used the name *Spongospora scabies* (Berkeley) Massee. Later the organism was studied cytologically by Osborn (1911 *a, b*) and Horne (1911); while Melhus (1914 *b*) and Kunkel (1915) have published on its life history.

When Brunchorst established the genus he saw a plasmodium-like stage associated with the spore balls, and regarded the organism as a relative of the slime moulds. Lagerheim opposed this point of view, and Maire and Tison failed to include the genus

in the Plasmodiophoraceae. Later workers have, however, generally regarded the organism as a member of this group.

Our knowledge of the life history of the species is considerably confused by contradictions in the accounts of Johnson, Horne, Osborn, and Kunkel. According to Johnson the spore germinates by eight zoospores, while Kunkel states that the entire content emerges as a single zoospore. Kunkel says further that the various zoospores which emerge from the spores composing a spore ball may coalesce to form a tiny plasmodium, and that this is capable of infecting the host by passing down into the tuber between its cells. In the host cell the behavior of the protoplast of the parasite seems to be much like that of other species of the family. At maturity several spore balls may exist together in the same cell. Osborn states that immediately preceding spore formation the nuclei fuse in pairs throughout the protoplast, and that this is followed by the reduction divisions. Additional investigation of the organism is desirable in the light of the evident contradictions in the published accounts.

The genus *Clathrosorus* Ferdinandsen and Winge (1920) was based on the single species, *C. campanulae* Ferd. & Wge. collected in Denmark on the roots of *Campanula rapunculoides.* The organism causes the formation of small galls resembling the legume tubercles. Spore balls somewhat resembling those of *Spongospora* were found, the individual spores having a minutely warted membrane. The "cruciform" type of nuclear division is pictured. The account is very brief, and knowledge of the life cycle too inadequate to warrant recognition of the genus. The organism is perhaps a relative of *Spongospora.*

Excluded Genera

The following genera, which have been incorporated in the Plasmodiophoraceae in certain recent treatments, are regarded as falling outside the limits of the group as here understood.

1. **Sporomyxa** Leger (1908).

An organism found in the coelomic cavity of the imago of *Scaurus tristis* was named *Sporomyxa scauri* Leger, and made the basis of this genus. Although Leger referred the species to the Plasmodiophoraceae its incorporation in the family does not seem justified. In addition to the fact that it occurs in an animal host, its possession of ellipsoidal spores indicates lack of

relationship. In any case our knowledge of its life cycle and cytology is insufficient to warrant its inclusion here.

2. **Ostenfeldiella** Ferdinandsen & Winge (1914: 648).

This genus was based on material collected by Ostenfeld on the coast of St. Croix (West Indies) on *Diplanthera wrightii* one of the Potamogetonaceae. The organism was found in the conspicuously thickened internodes of the erect branches, and was named *O. diplantherae* Ferd. & Wge. Certain cells of the host were found packed with brown, thick-walled spores. Uninucleate amoebae were found in others. Although other stages were not observed the organism was placed in the Plasmodiophoraceae by the authors of the new genus. There seems to be but slight reason for including it in the group, and at best its position is doubtful. The authors did not see living material.

3. **Cystospora** Elliott (1916: 15).

This genus was based by Elliott on a single species, *C. batata* Elliott, which he found to be the cause of a characteristic disease of the tubers of sweet potato called pox or soil-rot. Although he assigned the genus to the Plasmodiophoraceae there is in fact little in the published account to indicate relationship with this group.

Woroninaceae

Mycelium wholly lacking; thallus intramatrical, usually occurring in water moulds, in early stages existing as a naked, more or less amoeboid protoplast, at maturity, in some cases, forming a membrane and functioning as a single sporangium or resting spore, in others, fragmenting into a number of naked parts, each of which then assumes a membrane and functions as a sporangium or resting spore; the sorus, thus formed, consequently never provided with a soral envelope; sporangia typically multispored; zoospores laterally biciliate, as in the Oomycetes.

Key to Genera of Woroninaceae

I. Mature thallus functioning as a single sporangium or resting spore.
   A. Resting spore lacking a companion cell.
   1. **Pseudolpidium, p. 67**
   B. Resting spore bearing one or more companion cells.
   2. **Olpidiopsis, p. 67**

II. Mature thallus dividing to form a sorus of sporangia or resting spores, or functioning in its entirety as a resting spore.

A. Sporangia short-cylindrical, lying in a single row, filling the lumen of the host hypha; resting spores lying free as isolated, spiny spheres; each resting spore resulting from the transformation of an entire thallus.

3. **Rozella**, p. 68

B. Sporangia globose, lying free in the host cell and constituting a loose aggregation of indefinite form; resting spores similarly arranged or fused to form a warty cystosorus.

4. **Woronina**, p. 69

1. **Pseudolpidium** Fischer (1892: 33).

syn. *Olpidiopsis* (Cornu) Schröter (1892: 69).

Sporangium smooth-walled; resting spore spiny; companion cell lacking; swarmspores biciliate.

This genus and *Olpidiopsis* differ from *Olpidium* and *Pseudolpidiopsis* respectively of the following family chiefly in the biciliate character of their swarmspores. They are said to agree with the other members of the Woroninaceae in the absence of a membrane on the young thallus, but this point has not been thoroughly demonstrated. As the number of cilia on the swarmspore may be determined with certainty only in favorable material the separation of species of these corresponding genera involves accurate observation. A discussion of the interrelationships of the four genera is given below under *Olpidium.* The following are the best known species of *Pseudolpidium.*

P. saprolegniae (Braun) Fischer—in *Saprolegnia.*
P. fusiforme (Cornu) Fischer—in *Achlya.*
P. aphanomycis (Cornu) Fischer—in *Aphanomyces.*
P. pythii Butler—in *Pythium.*

2. **Olpidiopsis** (Cornu) Fischer (1892: 37).

syn. *Diplophysa* Schröter, subgenus *Euolpidiopsis* Fischer (in Schröter 1892: 85).

Sporangium smooth-walled; resting spore tuberculate or spiny; companion cell present; swarmspores biciliate; all known species parasitic in Saprolegniaceae.

The following species have been critically studied.

O. saprolegniae Cornu—in *Saprolegnia* (Fig. 7, *e*).
O. vexans Barrett—in *Saprolegnia* (Fig. 7, *a–d*).
O. minor Fischer—in *Achyla.*
O. aphanomycis Cornu—in *Aphanomyces.*
O. luxurians Barrett—in *Aphanomyces.*

3. **Rozella** Cornu (1872: 114).

A small genus containing two species, one *R. septigena* Cornu (Fig. 8) parasitic in threads of *Saprolegnia*, the other, *R. simulans* Fischer, in *Achlya*. After the entrance of the infecting swarmspore the parasite exists for a time as a naked protoplast indistinguishable from the protoplasm of the host. It grows at the expense of the host, and finally fills entirely the lumen of the host hypha. The formation of transverse septa divides the thallus into a single row of short cylindrical sporangia whose

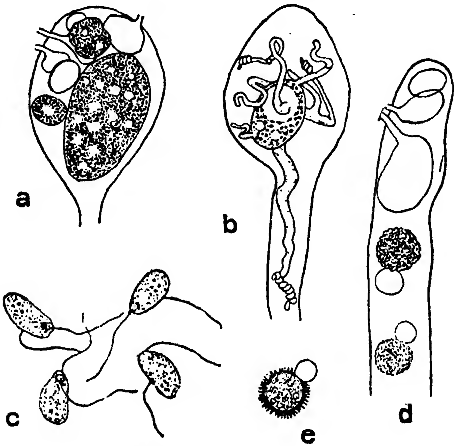

Fig. 7.—(*a–d*) *Olpidiopsis vexans* Barrett. (*c*) *O. saprolegniae* Cornu. (*a*) Swollen tip of hypha of *Saprolegnia* containing both emptied and unemptied swarmsporangia of the parasite. (*b*) Single sporangium with abnormal, long, coiled exit tubes. (*c*) Biciliate swarmspores. (*d*) Emptied swarmsporangia and verrucose resting spores with companion cells. (*e*) Spiny resting spore with companion cell. (*After Barrett 1912.*)

lateral walls are fused with the wall of the host. Each sporangium breaks up into a large number of biciliate swarmspores, and these escape through a short, usually lateral exit papilla. Other thalli assume the spherical form and develop into thick-walled spiny resting spores lying free in the host cell. They occur more often in short lateral branches which tend to become globose, and have in young stages the aspect of immature oogonia. The method of germination of the resting spore is unknown. No evidence of the existence of sexuality in the genus has been encountered.

4. **Woronina** Cornu (1872: 114).

The thallus in early stages is obscured by the protoplasm of the host, but later appears as a naked protoplast of variable form. The host lays down transverse septa confining it to a definite

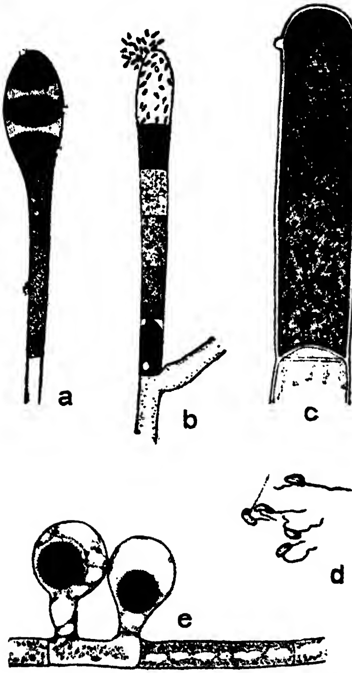

FIG. 8.—*Rozella septigena* Cornu in hyphae of *Saprolegnia*. (*a*) Linear series (sorus) of sporangia of Rozella in end of host hypha, lower three fully formed, terminal three developing at expense of host protoplasm. (*b*) Similar sorus, the terminal sporangium of which is freeing swarmspores. (*c*) Single terminal sporangium; the wall of the parasite distinguishable from that of the host where the lateral exit papillae are pushing out. (*d*) Swarmspores. (*e*) Spiny resting spores of *Rozella* lying in lateral host branches which are perhaps oogonia. (*After Cornu 1872.*)

short cell or compartment. Several such cells enclosing different thalli may form a linear series. At maturity the thallus, having absorbed completely the protoplasm of the host cell, fragments, forming a number of globose sporangia each of which then

assumes a thin smooth membrane. The sporangia lie in a loose cluster free from one another and only partially fill the host cell. Each sporangium at maturity frees a number of biciliate swarmspores through an inconspicuous exit papilla. Other thalli develop the resting stage. In *W. polycystis* Cornu occurring in

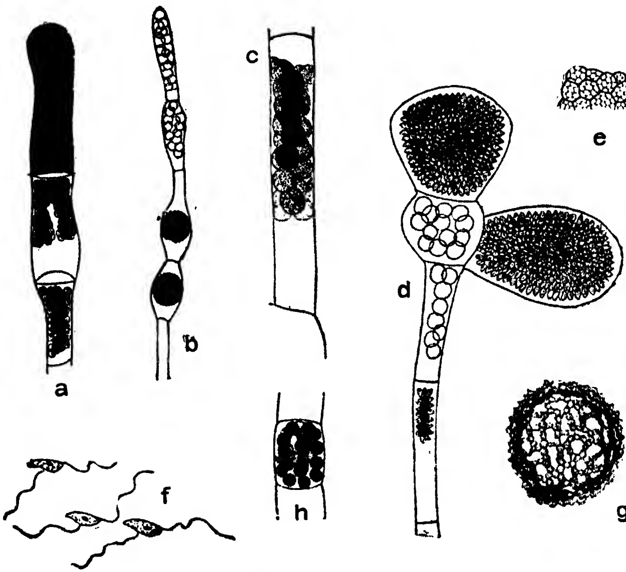

FIG. 9.—(*a-g*) *Woronina polycystis* Cornu in *Saprolegnia*. (*h*) *W. glomerata* (Cornu) Fischer in *Vaucheria*. (*a*) Host hypha with two sori of swarmsporangia, and at the tip a compartment in which the thallus of the parasite is as yet indistinguishable from the cytoplasm of the host. (*b*) Linear series of compartments, two containing sori of swarmsporangia and two cystosori. (*c*) Sorus of swarmsporangia. (*d*) Two sori of swarmsporangia and three cystosori, one unusually small. (*e*) Swarmspores delimited in sporangia. (*f*) Swarmspores. (*g*) Median section of cystosorus. (*h*) Sorus of resting spores. (*d*, and *f*, *after A. Fischer 1882*; *others after Cornu 1872*).

Saprolegnia the thallus fragments to form a number of resting spores but these fuse forming a single large thick-walled warty body termed the cystosorus (Fig. 9, *a–g*). In *W. glomerata* (Cornu) Fischer, in *Vaucheria*, each resting spore assumes a spiny wall, and a loose cluster of small spherical resting spores resembling the sporangial sorus results (Fig. 9, *h*).

The genus *Pyrrhosorus* Juel (1901: 14) founded on *P. marinus* Juel, a saprophyte in dead branches of *Cystoclonium purpurascens*, is imperfectly known, but seems to fall near *Woronina.*

Olpidiaceae

Mycelium wholly lacking; thallus intramatrical, provided from an early period with a thin membrane, at maturity functioning in its entirety as a single sporangium or resting spore; zoospores uniciliate; cilium at the posterior end of the spore.

Key to Genera of Olpidiaceae

I. Sporangium lying free in the host cell.
  A. Sporangium not provided with numerous exit tubes.
    1. Mature sporangium ellipsoidal to fusiform, lacking elongate exit tubes, dehiscing at one or both ends by a simple pore or short papilla.
      1. Sphaerita, p. 72
    2. Mature sporangium more or less globose.
      a. Resting spore globose to ellipsoidal, becoming stellate by shrinkage; sporangium sometimes dehiscing by a simple pore, sometimes by an exit tube.
        2. Olpidiaster, p. 72
      b. Resting spore not becoming stellate by shrinkage; sporangium dehiscing by one to few elongate exit tubes.
        (1) Resting spore not bearing a companion cell.
          3. Olpidium, p. 73
        (2) Resting spore bearing one or more companion cells.
          4. Pseudolpidiopsis, p. 76
  B. Sporangium with numerous exit tubes.
    1. Sporangium tubular; exit tubes short and arranged in a row.
      5. Ectrogella, p. 77
    2. Sporangium globose; exit tubes long and protruding in many directions.
      6. Pleotrachelus, p. 78

II. Sporangial wall tightly appressed to the wall of the host cell.
  A. Wall of host and that of parasite completely fused; no line of demarcation discernible between them; parasites on other fungi.
    7. Pleolpidium, p. 78
  B. Walls of host and parasite merely in contact, not fused; parasites in algae.
    8. Plasmophagus, p. 79

1. **Sphaerita** Dangeard (*Ann. Sci. Nat.* 7 ser. *bot.*, **4**: 277, 1886). (See also *Le Botaniste*, **1**: 46, *pl. 2–3;* **4**: 234, *fig. 7–8,* and *Bul. Soc. Bot. France*, **74**: 472, 1927.)

The genus was founded on *S. endogena* Dang. parasitic in *Euglena* and other Protozoa. As described by Dangeard the sporangium is ellipsoidal (Fig. 10, *a*, *b*) and opens by a pore.

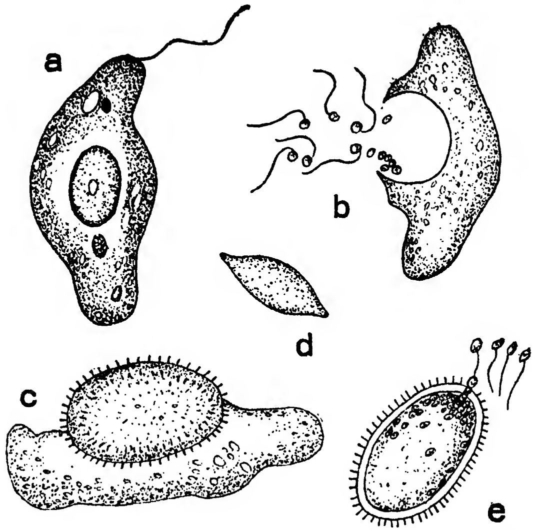

FIG. 10.—*Sphaerita endogena* Dangeard in *Euglena.* (*a*) Young swarmsporangium. (*b*) Germinating swarmsporangium. (*c*, *e*) Spiny resting sporangium. (*d*) Fusiform swarmsporangium. (*a, b, c, e, after Dangeard 1889; d, after Serbinow 1907.*)

In a later account by Serbinow (*Scripta Hort. Bot. Petrop.*, **24**: 154, *pl. 5*, 1907) it is pictured as fusiform, and is stated to have a short exit papilla at one or both ends (Fig. 10, *d*). Another species *S. trachelomonadis* Skvortzow (1927: 205) has been described from China in *Trachelomonas.*

2. **Olpidiaster** Pascher (*Beih. Bot. Centralbl.*, **35**²: 578, 1917).

syn. *Asterocystis* DeWildeman (*Ann. Soc. Belge Micros.*, **17**: 21, 1893); antedated by *Asterocystis* Gobi (1879), an algal genus.

A single species, *O. radicis* (De Wild.) Pascher, is included in the genus. It is parasitic on the roots of various plants, especially the Cruciferae, and causes chlorosis. The genus differs from *Olpidium* chiefly in the stellate aspect of the shrunken resting spore. As originally described the sporangia dehisce by a simple pore. Recently, however, Guyot (1927: 79) has figured sporangia of *O. radicis* provided with elongate exit tubes and the question of the advisability of merging this genus in *Olpidium* may well be raised. The wall of the resting spore in *Olpidiaster* is colorless.

The genus *Chrysophlyctis* Schilbersky was included in the Olpidiaceae by von Minden, and resembles *Olpidiaster* in having a resting sporangium which is somewhat stellate in form, though the wall differs in being dark colored. The genus is based on a single species, *Chr. endobiotica* Schilb., cause of the black wart of potato. Further investigation has shown that this species is in fact a *Synchytrium*, and it is discussed under that genus in the following family.

3. **Olpidium** Schröter (1886: 180).

The largest and best known genus of the family, containing about twenty-five species on a variety of substrata, including the tissue of higher plants, pollen grains, uredospores, mycelium of *Saprolegnia*, various algae, and lower animals. Both swarm-sporangia and resting spores are commonly developed. The former are relatively thin-walled, globose to ellipsoidal, and smooth. They germinate usually by a single prominent exit tube, which penetrates the host tissue, ruptures at its apex, and frees swarmspores. The resting spores are thicker-walled, smooth or verrucose, and also germinate by swarmspores. The following species are common.

O. brassicae (Wor.) Dang.—in cabbage (Fig. 11).
O. pendulum Zopf—in pollen in water.
O. endogenum (Braun) Schröter—in desmids.
O. uredinis (Lag.) Fischer—in uredospores of rusts.
O. zygnemicolum P. Magnus—in *Zygnema*.
O. entophytum Braun—in *Spirogyra*, *Vaucheria*, and *Cladophora*.
O. oedogoniarum (Sorokin) De Wildeman—in *Oedogonium*.

The genera *Olpidium* and *Pseudolpidiopsis* of this family and *Pseudolpidium* and *Olpidiopsis* of the preceding family should be discussed together since the similarity in form and aspect of

these fungi raises at once the question of their relationship. The generic limits used here are those adopted by von Minden (1911: 228, 260) and differ considerably from those of older authors. Schröter (1886: 195; 1892: 67, 84), in his treatment of these forms, includes in the genus *Diplophysa* all species in which the resting spore bears companion cells. He placed the remaining species in *Olpidium* and *Olpidiopsis*, including in *Olpidium* those with uniciliate zoospores and smooth-walled resting spores, and in *Olpidiopsis* those with biciliate zoospores and spiny resting spores. Fischer (1892: 16) recognized three genera corresponding in their limits with those of Schröter, but in his treatment the name *Pseudolpidium* replaces *Olpidiopsis* while *Olpidiopsis*

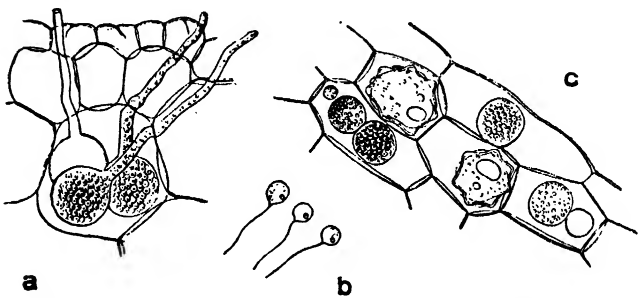

FIG. 11.—*Olpidium brassicae* (Woronin) Dangeard. (*a*) Three swarmsporangia with long exit tubes. (*b*) Swarmspores. (*c*) Roughened thick-walled resting spores. (*After Woronin 1878.*)

replaces *Diplophysa*. This confusing difference in application of generic names makes necessary a critical consideration of all the points involved.

The classification of von Minden (1911: 227) differs strikingly from older arrangements in the recognition of the new family Woroninaceae. In this family are placed those forms in which the zoospores are biciliate, and in which the thallus is naked in at least its early stages. The genera *Pseudolpidium* and *Olpidiopsis* included in the Woroninaceae, correspond respectively with *Olpidium* and *Pseudolpidiopsis* of the Olpidiaceae and differ from them only in the family characters.

The companion cell present on the resting spore in *Olpidiopsis* and *Pseudolpidiopsis* affords a morphological character useful in generic separation irrespective of the question of sexuality

involved. In these genera two thalli come in contact in early stages, one functioning as the male gametangium, the other as the female. The male individual, after discharging its contents through a pore connection into the female, remains attached to it, and is present later on the enlarged mature female cell (resting spore) as a small empty companion cell. In some cases more than one companion cell may be present. Those thalli which do not conjugate develop into thin-walled swarmsporangia. A critical cytological study of three species of *Olpidiopsis* was made by Barrett (1912), and his results indicate strongly that the two thalli which fuse show true sexual differentiation. He regards these fungi as primitive Oomycetes. The absence of a companion cell on the resting spore of *Olpidium* and *Pseudolpidium* does not on the other hand of necessity indicate a lack of sexuality in these forms. A fusion of ciliate gametes (resembling zoospores) has been observed in several cases and perhaps occurs in many species of these genera. In such cases complete fusion results in a zygote, there being no emptied male cell. Kusano (1912) has described the fusion of such swarmspore-like gametes in *O. viciae*, and finds that the zygote develops into a resting sporangium, while zoospores (without fusing) develop into swarmsporangia. It seems probable from the observations of Němec (1912) that the same type of life history exists in *O. brassicae*, and careful study will doubtless demonstrate it in other species. It was long ago observed by Fisch (1884: 17) in the two species on which he based the genus *Reesia*. In this genus ciliate zoospore-like gametes fuse in pairs outside the host. The zygote infects the host, and in it is amoeboid for a considerable period, finally maturing into a resting sporangium. Whether the nuclei fuse is not known. Von Minden (1911: 238, 243) does not recognize the genus, and incorporates the species under *Olpidium*. An imperfectly understood species occurring in the leaves of ragweed, and made by Griggs (1910: 50) the type of a new genus, *Monochytrium* Griggs, also probably belongs here. In this case the stages outside the host are unknown, but in the host cells, uninucleate amoeboid individuals fuse in pairs, the zygote finally being invested in a thick wall. Neither nuclear fusion nor germination of the resting spore was observed. The occurrence of planogamic copulation in these forms is of particular interest to the student of phylogeny since it demonstrates parallelism of the evolution of the sexual process between fungi

and algae down to the level of the most primitive forms. An interesting elaboration of this point is given by Ramsbottom (1914).

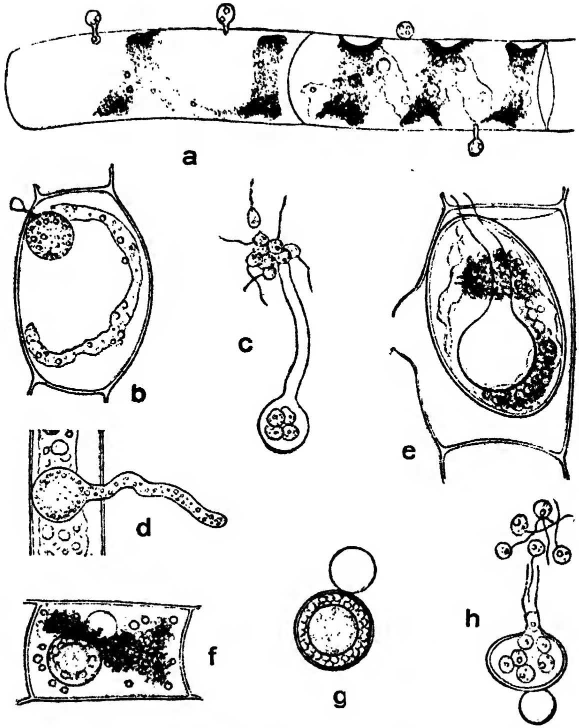

FIG. 12.—*Pseudolpidiopsis schenkiana* (Zopf) v. Minden in *Spirogyra*. (*a*) Encysted swarmspores germinating and accomplishing infection. (*b*) Young thallus developing from protoplast of swarmspore and still attached to the empty cyst wall. (*c–e*) Mature swarmsporangia. (*f*) After conjugation of two young thalli in a host cell. (*g*) Mature resting spore with companion cell. (*h*) Germinating resting spore. (*After Zopf 1884*).

4. **Pseudolpidiopsis** v. Minden (1911: 255).

syn. *Diplophysa* Schröter, subgenus *Pleocystidium* Fischer (in Schröter 1892: 85).

A single character, the presence of the companion cell on the resting spore, serves to separate this genus from *Olpidium*. The

two genera are evidently very closely related and should perhaps be merged. The first species enumerated below (Fig. 12) is the type of the genus. In it the resting spore is smooth-walled. The other species possess spiny-walled resting spores and have not been studied sufficiently to warrant their certain inclusion here. All of the species occur in green algae.

P. schenkiana (Zopf) v. Minden—in the filaments and zygospores of *Spirogyra*, *Mougeotia*, and *Mesocarpus*. Another form, *P. parasitica* (Fisch) v. Minden, said to differ in having several companion cells on the resting spore is perhaps the same.

P. zopfii (De Wild.) v. Minden and *P. fibrillosa* (De Wild.) v. Minden occur in *Spirogyra* and differ chiefly in the character and arrangement of the spines which ornament the resting spore.

P. appendiculata (De Wild.) v. Minden and *P. elliptica* (Schröter) v. Minden occur in *Mesocarpus*. The companion cell of the first is vermiform, that of the latter globose.


a

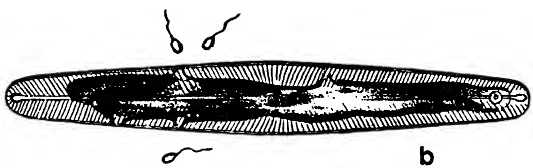
b

Fig. 13.—*Ectrogella bacillariacearum* Zopf in the diatom *Pinnularia*. (*a*) Young ellipsoidal thallus. (*b*) Germinating swarmsporangium provided with four exit tubes. (*After Zopf 1884.*)

In this genus, as in *Olpidiopsis* and other genera of the Chytridiales in which sexuality occurs, the resting spore has received various names (*e.g.*, resting sporangium, oospore, oosporangium), but it should be noted that the wall of the mature spore is merely the thickened or modified membrane of the female gametangium. An oospore lying free in the oogonium, as in the Ancylistales and Oomycetes, is never formed.

5. **Ectrogella** Zopf (1884: 175).

Erected on *E. bacillariacearum* Zopf, parasitic in diatoms and first observed by Zopf near Berlin. It also occurs in America

(Atkinson 1909 *a*: 338). The swarmsporangia are usually slender and vermiform, and put out as many as ten short exit tubes arranged in one or two definite rows (Fig. 13, *b*.). Resting spores are unknown. Another species, *E. perforans* Petersen (1905: 466), is described from Denmark in *Licmophora* and *Synedra*, and several other species on the same or related hosts have been described by Scherffel (1925: 10).

6. **Pleotrachelus** Zopf (1884: 173).

This genus was founded on a single species, *P. fulgens* Zopf, occurring in *Pilobolus*. In parasitized host plants sporangia, normally present, are suppressed and only zygospores are

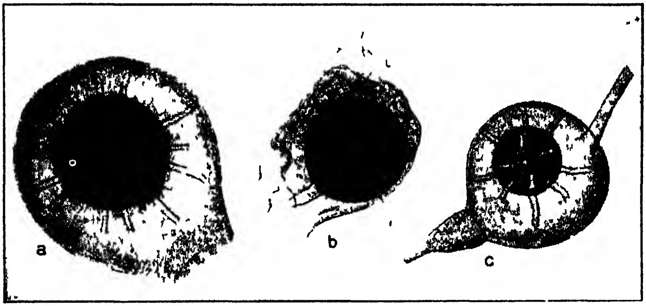

FIG. 14 — *Pleotrachelus fulgens* Zopf in *Pilobolus* (*After Zopf 1884*.)

developed. The sporangia of the parasite are globose and resemble those of *Olpidium* but differ in emitting a number of long slender exit tubes which protrude in many directions (Fig. 14). About ten other species have been described from algae and roots of higher plants (*Saccardo, Sylloge Fungorum*, **21: 24**).

7. **Pleolpidium** Fischer (1892: 43).

The members of this genus occur as parasites in the hyphae or sporangia of various relatively rare water moulds. The outstanding character of the genus is indicated in the derivation of the name *Pleolpidium* (*pleos*: filled, and *Olpidium*), which refers to the tendency of the parasite to fill the host cell. In those species which occur in the sporangium of the host the thallus enlarges until it completely fills the sporangium, the wall

of the parasite being so tightly appressed to that of the host that no line of separation between the two is visible. Consequently, a parasitized host sporangium may be easily mistaken for a normal one. The species occurring in the hyphae of the host stimulate the formation of pronounced fusiform or ellipsoidal enlargements, and the thallus at maturity completely fills the lumen of the hypha at the point of its enlargement. The thallus then functions as a swarmsporangium. It is thin-walled, smooth and hyaline, and forms one or more inconspicuous, short exit tubes indefinite in position. Other thalli develop into resting spores. These lie free in the host cell as brownish spheres, and have a thick, finely echinulate wall. In its relation to the host cell the thallus resembles that of *Rozella* of the Woroninaceae but in that genus fragmentation of the thallus at maturity results in the formation of a sorus of sporangia, while the swarmspores are biciliate. The following species are the best known.

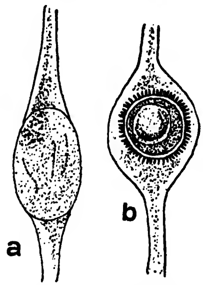

FIG. 15.—*Pleolpidium monoblepharidis* (Cornu) Fischer in fusiform enlargements of hyphae of *Monoblepharis.* (*a*) Thallus of parasite. (*b*) Resting spore of parasite. (*After Cornu 1872.*)

P. araiosporae (Cornu) v. Minden—in sporangia of *Araiospora.*
P. apodyae (Cornu) Fischer—in sporangia of *Apodachlya.*
P. blastocladiae v. Minden—in sporangia of *Blastocladia.*
P. monoblepharidis (Cornu) Fischer (Fig. 15)—in hyphae of *Monoblepharis.*
P. cuculus Butler—in sporangia of *Pythium.*

8. **Plasmophagus** De Wildeman, (*Ann. Soc. Belge Micros.*, **19**: 219, 1895).

A single species, *P. oedogoniorum* DeWild., in the vegetative cells of *Oedogonium*, comprises this genus. Resting spores have not been observed. The thallus tends to fill the host cell as in the preceding genus, but the two walls remain distinct. The thallus enlarges as the host thread develops, and failure of the latter to form the usual cross walls may result in a long cell filled by the parasite. Sometimes several thalli occur in the same host cell. The thallus at maturity functions as a sporangium, and uniciliate swarmspores escape through a short inconspicuous papilla. The sporangial wall is assumed relatively late, the naked protoplast, in early stages, being indistinguishable from that of the host.

Synchytriaceae

Mycelium wholly lacking; thallus intramatrical, provided from an early period with a membrane, at maturity either functioning in its entirety as a resting sporangium, or divided by cleavage planes to form a sorus of sporangia enclosed in a common soral membrane; zoospores uniciliate; cilium at the posterior end of the spore.

Key to Genera of Synchytriaceae

I. Resting spore relatively large; parasites in higher plants.
1. **Synchytrium**, p. 80

II. Resting spore very small; parasites in algae.
2. **Micromyces**, p. 87

1. **Synchytrium** de Bary & Woronin (1863: 22).

Probably no other genus of the Chytridiales is as widely known as *Synchytrium*. It is cosmopolitan in range, and several of its members are of considerable economic importance. The species are all parasitic in higher plants and cause noticeable galls.

The most extensive and satisfactory taxonomic treatment is that of Tobler (1913), but the monographs of Fischer (1892: 45) and von Minden (1911: 287) will also be found useful. Much work remains to be done before we will have a satisfactory knowledge of specific limits.

The genus may be split into four apparently natural groups of species, and these are treated here as subgenera.

I. Resting spores unknown; mature thallus functioning as a summer sorus of thin-walled sporangia; sporangia delimited within the thallus wall and freed by its rupture.
subgenus **Woroninella**

II. Resting spores known.
A. Life cycle embracing summer sori and the resting spore; the latter in germination functioning as a single sporangium and freeing swarmspores directly without the extrusion of a vesicle.
1. The sporangia of the summer sorus delimited within the thallus wall and freed by its rupture.
subgenus **Eusynchytrium**
2. The thallus functioning as a prosorus and extruding a thin-walled vesicle into which the protoplast flows and in which the sporangia are then delimited.
subgenus **Mesochytrium**

B. Summer sori not formed; resting spore in germination functioning as a prosorus, and extruding the endospore as a thin-walled vesicle in which the sporangia are then delimited.
subgenus **Pycnochytrium**

We are ignorant of the life cycles of a considerable number of species but apparently the majority belong to *Pycnochytrium*. De Bary gave this group generic rank and Schröter (1892: 73) follows the same procedure. In the present incomplete state of knowledge it would seem that nothing is to be gained by removing any of the forms from *Synchytrium*. Considerable doubt exists as to just how much importance is to be attached to the differences in sporangial formation which constitute the basis for the above key to subgenera. If the extrusion of the thin-walled vesicle should prove to be inconstant in some species, as has been shown to be the case in *Phytophthora*, the above separation could not be maintained. In any case, the genus as it stands constitutes a coherent whole.

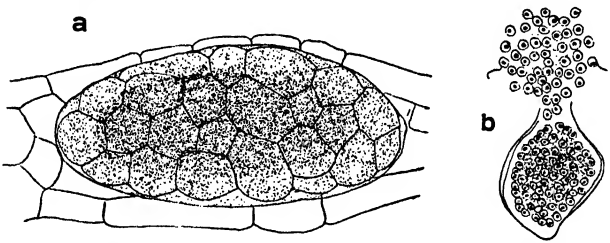

FIG. 16.—*Synchytrium taraxaci* de Bary & Woronin on *Taraxacum*. (*a*) Sorus of swarmsporangia. (*b*) Single swarmsporangium, more enlarged, germinating. (*After de Bary and Woronin 1865.*)

As representative of the subgenus *Eusynchytrium* the species, *S. taraxaci* de Bary & Woronin (1863: 22), occurring in Europe, Australia, and North America on *Taraxacum*, may be discussed (Fig. 16). In it several generations of swarmspores are formed during the summer, and only the last develop into resting spores. The earlier generations form summer sori of sporangia. The sorus is enclosed in a definite membrane, and at maturity contains fifteen to twenty sporangia. Though there is usually only one sorus in a single host cell there may be several. The sporangia are very unequal in size, are irregularly polyhedral from mutual pressure, and when fully formed have a thick hyaline wall and reddish orange contents. The swarmspores are freed on the living host and reinfect it. Each swarmspore is globose, uniciliate, and contains one or more reddish oil globules. The resting spore formed at the close of the season lies free in the host cell, is globose, and at maturity is provided

with a thick brown exospore and a thin hyaline endospore. Germination occurs in the spring, both walls rupturing without the extrusion of the endospore, and numerous swarmspores being freed directly. If sexuality is concerned in resting spore formation it has never been demonstrated. Another well known species belonging to the subgenus *Eusynchytrium* is *S. fulgens* Schröter occurring on *Oenothera*.

The best known member of the subgenus *Mesochytrium* is *S. endobioticum* (Schilbersky) Percival, cause of the much feared and destructive disease of potatoes known as black wart (Fig. 17) introduced into the United States from Europe (Orton 1919;

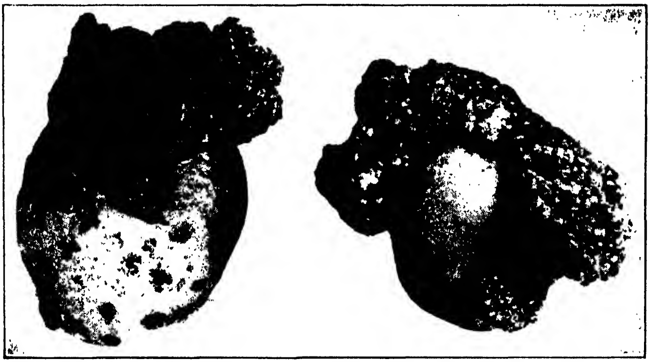

FIG. 17.—*Synchytrium endobioticum* (Schilb.) Percival, cause of "black wart" disease of potatoes. (*Photograph by McCubbin.*)

Hartman and McCubbin 1924). This species was made the basis of a new genus by its discoverer Schilbersky, being named by him *Chrysophlyctis endobiotica* Schilb. The genus was included by von Minden (1911: 228) in the Olpidiaceae where it was separated from the other genera of the family by the strikingly angular form of the resting spore. The position of the species in classification was for a time in controversy, but its inclusion by Percival in *Synchytrium* has been justified by the results of more recent research. The genus *Chrysophlyctis* therefore disappears. The following discussion of the morphology and life history of the species is based largely on the account of Curtis (1921: 409). Her paper is of unusual interest in that she shows that the resting spore in this species results from a sexual fusion of motile isoga-

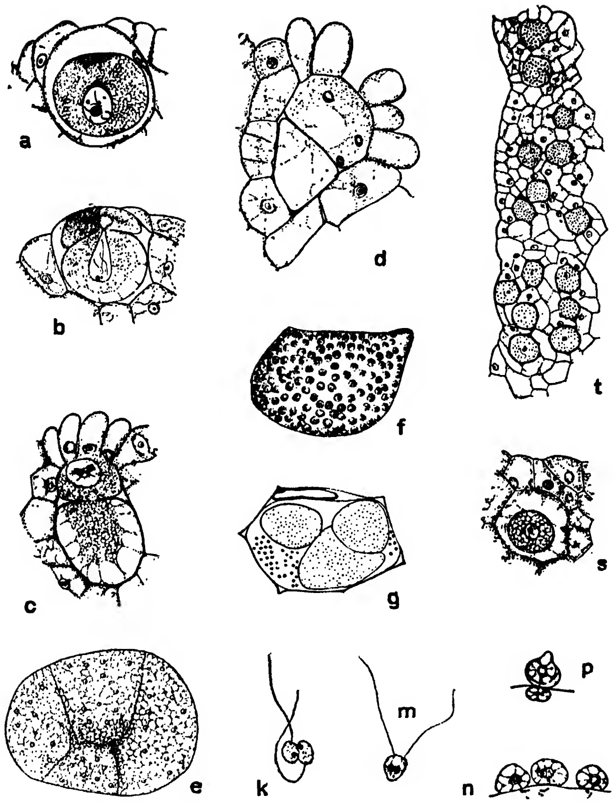

FIG. 18.—*Synchytrium endobioticum* (Schilb.) Percival. (*a*) Uninucleate thallus. (*b*) Thallus functioning as a prosorus; its contents streaming out into a thin-walled vesicle, the sorus. (*c*) Uninucleate sorus. (*d*) Sorus plurinucleate by division of primary nucleus. (*e*) Cleavage planes have divided the sorus into sporangia and repeated nuclear division has occurred. (*f*) Mature sporangium; papilla of dehiscence forming. (*g*) Three mature sporangia in a common soral membrane; swarmspores escaping; the old prosoral envelope flattened against the host wall. (*k*) Two gametes in contact. (*m*) Binucleate zygote following fusion. (*n*) Zygotes encysted on host wall; the cilia have disappeared and nuclear fusion has occurred.. (*p*) Infection by zygote. (*s*) Young resting sporangium. (*t*) Epidermal region of gall containing resting spores (resting sporangia) near maturity. (*After Curtis 1921.*)

metes (Fig. 18, *k*, *m*). In the accounts of early workers on the Synchytriaceae so many references to the observation of giant biciliate swarmspores occur that a sexual fusion of ciliate cells has long been suspected. The demonstration of its occurrence in this species makes logical the assumption that the resting spores of other species are also truly sexual in nature. In this connection the discussion of planogamic copulation given above (p. 81) should be read. In this species, as in *S. taraxaci* discussed above, both summer sori and resting spores are formed. The resting spore in germination produces swarmspores directly. These infect the host and produce thalli which at maturity function as prosori. The prosorus is provided with a thick orange exospore and a thin hyaline endospore. At first it is uninucleate (Fig. 18, *a–c*). The cytoplasm and nucleus pass out into a vesicle consisting of the extruded endospore, and in this vesicle nuclear division occurs, approximately a dozen nuclei being formed before the sporangia are delimited. The sporangial walls are formed simultaneously and independent of the nuclei, about four to nine sporangia composing the sorus. The extrusion of the endospore occurs while the fungus still lies in the host cell, and the exospore may be flattened out at one side by the pressure exerted by the protoplast, and at maturity be relatively inconspicuous. Nuclear divisions continue in the sporangia until two hundred to three hundred nuclei are formed in each. The enlarging sporangia exert sufficient pressure to finally rupture the soral membrane and the wall of the host cell, and are thus set free. Then one or two hyaline papillae are formed on each sporangium, and, at the rupture of one of these, numerous uninucleate motile cells escape. Some of these motile cells function as swarmspores and after infecting the host develop into other prosori. Some of them function as gametes and fuse in pairs, the resulting zygote penetrating into the host and developing there into a resting sporangium. It is probable that the two gametes which fuse originate in different sporangia, though the point is difficult to demonstrate. Their nuclei fuse in the zygote before infection occurs. The mature resting spore swells by the imbibition of water and bursts, freeing swarmspores directly. Other species belonging in the subgenus *Mesochytrium* are *S. succisiae* de Bary & Woronin on *Succisa*, *S. cellulare* Davis (1924: 287) on *Lycopus*, and *S. stellariae* Fuckel on *Stellaria*. In the subgenera *Eusynchytrium* and *Mesochytrium* few data are available concern-

ing the germination of the resting spore. Though it is assumed that it frees swarmspores directly in all the species, it may yet be shown to function in some as a prosorus as in *Pycnochytrium*.

The species of *Pycnochytrium* may be separated into two groups, those in which the contents of the resting spore are colored (*Chrysochytrium*) and those in which they are hyaline (*Leucochytrium*). Eight or nine species may be placed in each group with certainty, and there are many other doubtful forms. Throughout the subgenus the resting spore functions in all known cases as a prosorus, the sporangia being formed in an extruded vesicle. Summer sori are not formed in any case. Perhaps the best known species of the subgenus is *S. aureum* Schröter. While most species are limited to a few hosts this one occurs on no fewer than one hundred and thirty plants representing such widely separated genera as *Viola*, *Ulmus*, *Trifolium*, *Solidago*, and *Mentha*. None of the species of *Pycnochytrium* is of any great economic importance. The following occur in North America:

S. aureum Schröter—on many hosts.
S. myosotidis Kühn—on *Lithospermum*.
S. anemones (DC.) Woronin—on *Anemone*.
S. anomalum Schröter—on *Adoxa*.
S. holwayi Farlow—on *Monarda*.
S. mercurialis (Libert) Fuckel—on *Oenothera*
S. cinnamomeum Davis—on *Ranunculus*.

The three subgenera *Eusynchytrium*, *Mesochytrium*, and *Pycnochytrium* constitute the genus in the older treatments. To these Gäumann (1927: 169) has recently added the fourth, *Woroninella*.

Raciborski (1898) erected the genus *Woroninella* Rac. on a single species, *W. psophocarpi* Rac., occurring in Java on *Psophocarpus tetragonolobus* DC. He states that it differs from *Synchytrium* in the possession of biciliate swarmspores. He regarded it as intermediate between *Woronina* and *Synchytrium*. Later he (Raciborski 1900: 7) added another species, *W. vulcanica* Rac., found on *Lespedeza*. Both of these fungi cause galls on their hosts, and in general resemble species of *Synchytrium*. Sydow (1914) then transferred to *Woroninella* five species previously incorporated in *Synchytrium* by other authors including *S. aecidioides* (Peck) Lag. and *S. puerariae* (Hennings) Miyabe. The group of forms thus brought together resemble one another in the absence of a thick-walled resting spore and in the powdery

aspect of the open sorus of swarmsporangia. This latter characteristic led earlier investigators to mistake these fungi for rusts. In fact several species were first described in *Aecidium* and *Uredo.*

The common North American representative of the genus, *W. aecidioides* (Peck) Sydow, was first described by Peck in the genus *Uredo.* It was later placed in *Synchytrium* by Farlow, and will be most frequently encountered in the literature under the name *S. decipiens* Farlow. The species occurs in America on the hog peanut, *Amphicarpa monoica* and *A. pitcheri,* and in Oriental India and Japan on *A. edgeworthii.* It is probably the best known representative of the Chytridiales in the United States. It has been studied cytologically by Harper (1899), Stevens (1903; 1907), and Griggs (1908; 1909 *a, b, c*). The infecting swarmspore is uninucleate, and the uninucleate condition is maintained in the developing thallus until it approaches maturity. This nucleus, termed the primary nucleus, enlarges rapidly as the thallus grows, and finally attains an extraordinary size. It then divides to form nuclei for the sporangia, and these in turn, after the sporangial walls are initiated, divide to provide nuclei for the swarmspores. The species forms galls on the leaves, stems, and other aerial portions of the host, and may sometimes be found even on the fleshy subterranean pods of the lower flowers. The species is clearly very closely related to *W. puerariae* (Hennings) Sydow occurring in the Far East on *Pueraria.*

Kusano (1909: 86, 112) studied the latter species very critically, and found the swarmspores to be uniciliate. He, consequently, followed the nomenclature of Miyabe (1905: 199) who had first placed the species in *Synchytrium.* Later Ito and Homma (1926) confirmed this finding, and demonstrated that the swarmspores are uniciliate in *W. aecidioides* also. Since these two species fail to show the swarmspore character described for *Woroninella,* and since the open powdery nature of the sorus is not typical of *Synchytrium* they erected a new genus *Miyabella* Ito and Homma for them.

The following year Gäumann (1927) examined the type species of *Woroninella, W. psophocarpi,* and proved that in it also the swarmspores are uniciliate. There is no longer, therefore, any reason for retaining the genus *Woroninella.* Nevertheless, since the group of species here treated differ from the other known species of *Synchytrium* in the strikingly powdery aspect of their

open aecidium-like sori and in the absence of the resting spore stage it would seem that Gäumann's erection of the subgenus *Woroninella* was warranted. It is possible that further study will make desirable merging the group with *Eusynchytrium*.

North American species of *Synchytrium* not listed above because of their uncertain position in the genus include the following.

S. asari Arthur & Holway—on *Asarum*.
S. caricis Tracy & Earle—on *Carex*.
S. innominatum Farlow—on *Malacothrix*.
S. nigrescens Davis—on *Aster*.
S. scirpi Davis—on *Scirpus*.
S. vaccinii Thomas—on *Vaccinium, Kalmia, Cassandra*, etc.

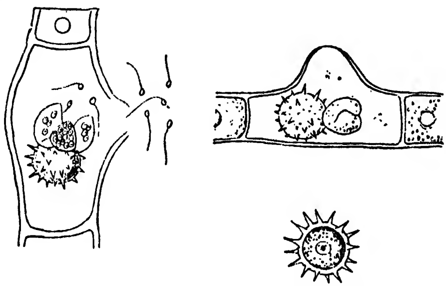

FIG. 19.—*Micromyces zygogoni* Dangeard in *Zygogonium*. (*After Dangeard 1889.*)

2. **Micromyces** Dangeard (*Le Botaniste*, **1**:55, 1889).

A small and imperfectly understood genus included here as a doubtful member of the family. The genus was based by Dangeard on a single species, *M. zygogoni* Dang. (Fig. 19), found in France in the cells of the alga *Zygogonium*. Subsequently several other species have been described from other algae. These include *M. mesocarpi* DeWildeman in *Mesocarpus* in Belgium, *M. spirogyrae* Skvortzow in *Spirogyra* in China, and *M. petersenii* in *Mougeotia* in Czechoslovakia.

The mature thallus is a small sphere. It becomes invested in a coarsely spiny membrane, and functions as a resting spore. In germination it either frees zoospores directly, or, as in the subgenus *Pycnochytrium* of *Synchytrium*, its contents pass into a thin-walled vesicle and there form a small sorus of sporangia which in turn form zoospores.

The genus *Micromycopsis* Scherffel (1926: 167) based on *M. cristata* Scherffel in *Hyalotheca* and *M. fischerii* Scherffel in *Zygogonium* should be considered in this connection.

Rhizidiaceae

Although this family contains a larger number of genera than any other in the order it is probably the least well known. The forms are chiefly transient in character, and are with difficulty kept under observation long enough for the completion of satisfactory studies. The members of the group vary greatly in morphology, and present many interesting features whose further elucidation will tend to shed light on the general problem of phylogeny in the order (see key, p. 48).

In the following key the essential characters of the genera are indicated, and to avoid unnecessary repetition these are omitted in the text. For a more detailed taxonomic treatment the student should consult von Minden (1911) or Fischer (1892). It is highly probable that many as yet undescribed species exist in nature.

Key to Cenera of Rhizidiaceae

I. Mycelium wholly intramatrical.
  - A. Sporangia epibiotic.
    - 1. Mycelium consisting of delicate, more or less branching threads.
      - a. Resting spores when present epibiotic.
        - (1) Mycelium usually monophagus; resting spore germinating by swarmspores.
          - (a) Sporangium lacking a subsporangial vesicle.
            - 1. **Rhizophidium**, p. 91
          - (b) Sporangium provided with a subsporangial vesicle.
            - 1′. Sporangium with an extramatrical stalk.
              - a′. Sporangium with a solid apical spine; the stalk in open connection with the sporangium; saprophytes.
                - 2. **Obelidium**, p. 92
              - b′. Sporangium lacking the apical spine, separated by a septum from the stalk; parasites.
                - 3. **Podochytrium**, p. 92

2′. Sporangium lacking an extramatrical stalk.

a′. Swarmspores freed through an apical opening.

1″. Sporangium opening by a large lid; resting spore formed by a definite sexual process in which a male individual sends a fertilization tube into a female individual.

4. **Zygorhizidium**, p. 93

2″. Sporangium not opening by a lid.

a″. Contents of sporangium escaping into a thin-walled vesicle in which the swarmspores are then formed.

5. **Rhizidiomyces**, p. 93

b″. Swarmspores formed in the sporangium.

1‴. Swarmspores encysting at the mouth of the sporangium as in *Achlya*.

6. **Achlyella**, p. 94

2‴. Swarmspores escaping without encystment.

7. **Phlyctochytrium**, p. 94

b′. Swarmspores freed through a basal or subbasal opening.

1″. Sporangial wall spiny.

8. **Asterophlyctis**, p. 94

2″. Sporangial wall smooth.

a″. Mycelial threads drawn out to extremely slender tips.

9. **Rhizoclosmatium**, p. 94

b″. Mycelial threads more definitely tubular.

10. **Siphonaria,** p. 95

(2) Mycelium often wide-spreading, saprophytic; resting spore in germination functioning as a prosporangium, the swarmspores being delimited in the extruded endospore.

11. **Rhizidium,** p. 96

b. Resting spores intramatrical.

12. **Dangeardia,** p. 96

2. Mycelium not consisting of delicate threads.

a. Mycelium consisting of a delicate stalk flattened at its tip to form a small disc which is either applied to or developed in the host wall; sporangia long, fusiform, proliferating.

13. **Harpochytrium,** p. 96

b. Mycelium not forming such a disc.

(1) Resting spore endobiotic, germinating to form an epibiotic sporangium; mycelium consisting of a short broad tube.

14. **Chytridium,** p. 96

(2) Resting spore epibiotic, germinating by swarmspores.

(a) Contents of sporangium escaping into a thin-walled vesicle in which the swarmspores are then formed; mycelium consisting of a lobed or slightly divided haustorium.

15. **Saccomyces,** p. 98

(b) Sporangium not extruding a vesicle; mycelium consisting of an unbranched filiform or bladder-like haustorium.

16. **Phlyctidium,** p. 98

B. Sporangia and resting spores intramatrical, developing from a swelling formed at the tip of the germ tube of the swarmspore.

1. Sporangia and resting spores lacking a subsporangial vesicle. Resting spore wall smooth.

17. **Entophlyctis,** p. 98

2. Subsporangial vesicle present; resting spore wall spiny.

18. **Diplophlyctis,** p. 98

II. Only the tips of the branches of the mycelium intramatrical, entering several host cells (polyphagus), parasitic.

A. Individual functioning as a sporangium or resting spore.

1. Swarmspores freed from the sporangium through a definite opening.

19. **Rhizophlyctis,** p. 99

2 Swarmspores freed by disintegration of the sporangial wall and remaining together for a time as a rotating sphere
20 **Nowakowskia,** p 99

B. Individual functioning as a prosporangium, its contents extruded into a thin-walled vesicle in which the spores are formed Resting spore formed as a result of the copulation of two individuals
1 Sporangiospores non-motile, germinating in the sporangium as in *Aplanes*
21 **Sporophlyctis,** p 100

2 Sporangiospores ciliated and escaping before germination
22 **Polyphagus,** p 100

1 **Rhizophidium** Schenck (Über Vorkommen Kontraktiler Zellen 1858).

A large genus of about thirty species occurring in the water on algae, lower fungi, lower animals, pollen grains (Fig 20), and similar substrata. A key to most of the known species is given

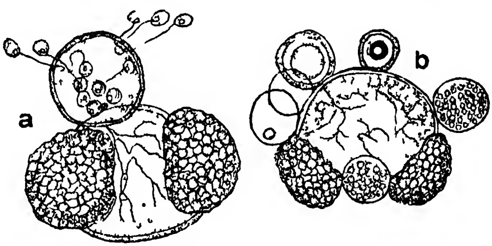

Fig 20—*Rhizophidium pollonis* (A. Braun) Zopf, on pollen grains (*a*) Swarmsporangium and swarmspores (*b*) Two resting spores and four swarmsporangia, two of which have freed their spores (*After Zopf 1888*)

by von Minden (1911: 316). Notes of particular interest to American students are given by Atkinson (1894, 1909 *a*), Coker (1923: 186), Martin (1922), Melhus (1914 *a*), and Zeller (1918). In the search for chytrids in algae, members of this genus are more often encountered than other forms, *R. globosum* (Fig. 21) being particularly common.

The genus *Latrostium* Zopf (1894), erected on *L. comprimens* Zopf occurring on *Vaucheria*, resembles *Rhizophidium* in the form of the swarmsporangium. The statement that the cilium precedes the swarmspore in swimming raises a question as to the actual relationships of the form, and it is here treated as doubtful (see key, p 48).

2 **Obelidium** Nowakowski (1876 86)

Erected on the single species, *O mucronatum* Nowak , occurring in Europe on larvae and nymphs lying in the water (Fig 22)

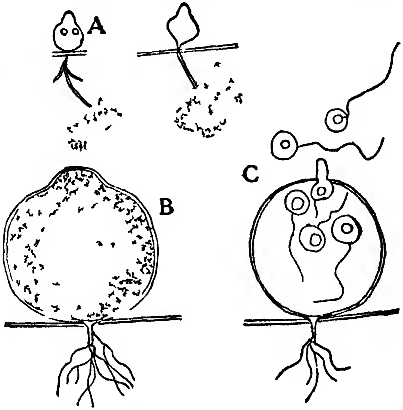

Fig 21 —*Rhizophidium globosum* (A Braun) Schroter *A* Young plant developed from encysted swarmspore the penetration tube forming rhizoids *B* Mature plant *C* Plant functioning as a swarmsporangium and freeing swarmspores (*After Atkinson 1909*)

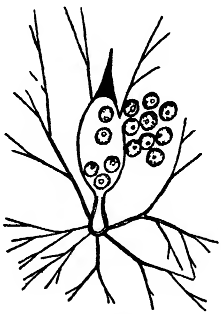

Fig 22 —*Obelidium mucronatum* Nowakowski Sporangium with a solid apical spine swarmspores escaping through a subapical lateral pore (*After Nowakowski 1876*)

3 **Podochytrium** Pfitzer (Sitzungsber Nieder-rhein Ges Natur und Heilkunde pp 62, Bonn 1870)

Erected on the single species, *P clavatum* Pfitzer, occurring in *Pinnularia* The same thing was described and well figured by Zopf (1888) under the name, *Septocarpus corynephorus* (Fig 23).

4. **Zygorhizidium** Lowenthal (*Archiv fur Protistenkunde*, **5**: 228, *pl 8*, 1904)

Erected on the single species, *Z willei* Lowenthal, in *Cylindrocystis* in Norway

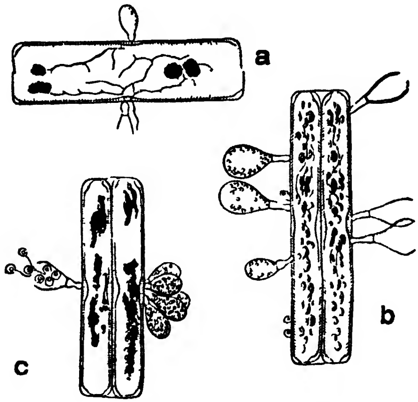

FIG 23 *Podochytrium clavatum* Pfitzer in *Pinnularia* (*a*) Young plant (*b c*) Mature plants showing subsporangial extramatrical stalk (*After Zopf 1888*)

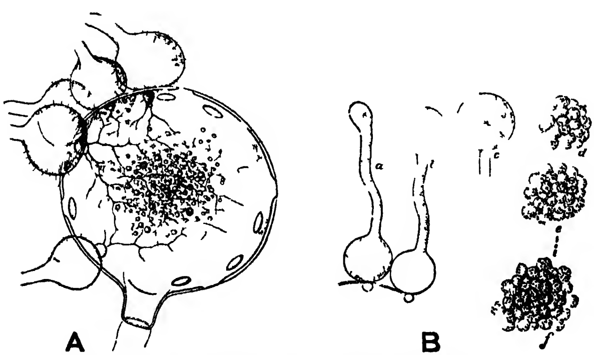

FIG 24 —*Rhizidiomyces apophysatus* Zopf in oogonium of *Achlya* *A* sporangia *B* stages in swarmspore formation (*After Zopf 1884*)

5 **Rhizidiomyces** Zopf (1884 188)

Two species, *R apophysatus* Zopf (Fig 24), in the oogonia of *Achlya* and *Saprolegnia*, originally described from Europe and

reported by Coker (1923: 186) from North America, and *R. ichneumon* Gobi in *Chloromonas*.

6. **Achlyella** Lagerheim (*Hedw.* **29**: 143, 1890).

Erected on the single species, *A. flahaultii* Lag., found in pollen grains of *Typha* in water.

7. **Phlyctochytrium** Schröter (1892: 78).

A relatively large genus containing over a dozen species occurring chiefly as parasites in algae. Except in the possession

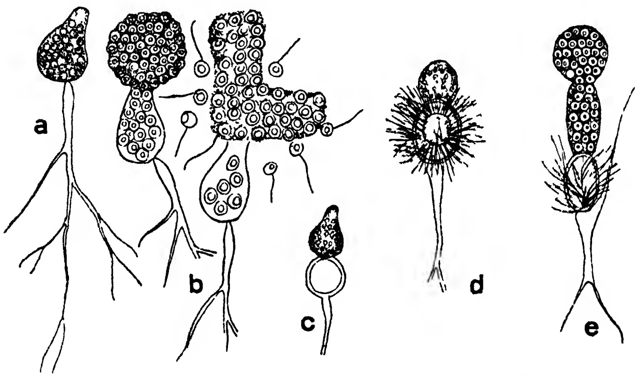

FIG. 25. *Rhizidium mycophilum* A. Braun in slime of *Chaetophora*. (*a*) Branching thallus bearing a sporangium. (*b*) Sporangia freeing swarmspores (*c*) Smooth-walled resting sporangium functioning as a prosporangium. (*d*) Hairy resting sporangium. (*e*) Same functioning as a prosporangium (*After Nowakowski 1877.*)

of a subsporangial vesicle the genus corresponds to *Rhizophidium*. Resting spores are unknown. Two species, *P. planicorne* Atk. and *P. equale* Atk., have been found in North America (Atkinson 1909 *a*) on *Spirogyra*.

8. **Asterophlyctis** Petersen (*Jour. de Botanique,* **17**: 218, 1903).

Erected on a single species, *A. sarcoptoides* Petersen, saprophytic in empty nymph cases lying in water.

9. **Rhizochlosmatium** Petersen (*Jour. de Botanique,* **17**: 216, 1903).

Erected on a single species, *R. globosum* Petersen, saprophytic in empty nymph cases lying in water.

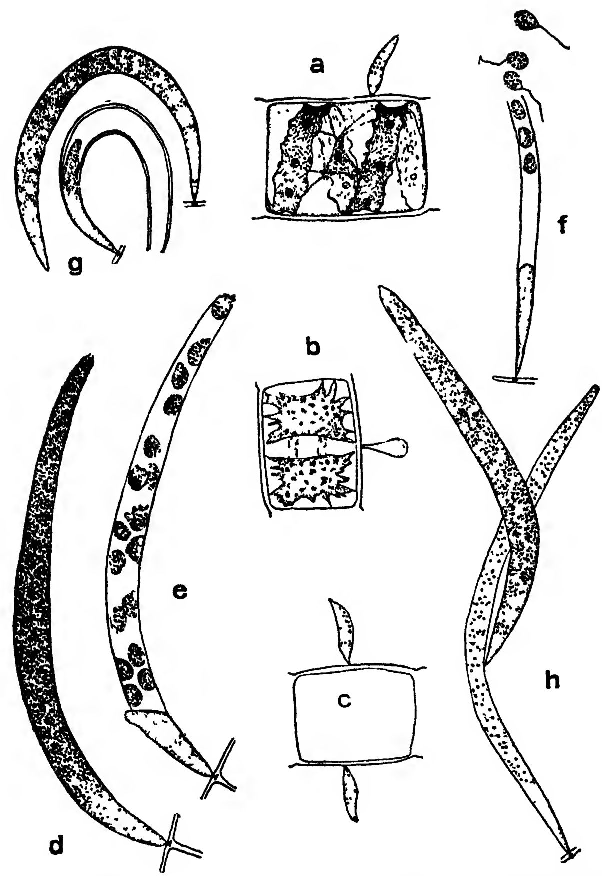

FIG. 26.—*Harpochytrium hedenii* Wille on *Spirogyra* and *Zygnema* (*a–c*) Young thalli developed from swarmspores. (*d*) Mature plant. (*e*) Zoospores escaping in amoeboid state; secondary sporangium forming below primary. (*f, g*) Uniciliate swarmspores escaping; proliferation of sporangia. (*h*) One individual of *Harpochytrium* attacked by another. (*After Atkinson 1903.*)

10. **Siphonaria** Petersen (*Jour. de Botanique*, **17**: 220, 1903).

Erected on a single species, *S. variabilis* Petersen saprophytic in empty nymph cases lying in water.

11. **Rhizidium** A. Braun (Monatsber. Berl. Akad., p. 591, 1856).

Several species described from Europe include, R. *mycophilum* A. Braun (Fig. 25), in slime of *Chaetophora*, *R. lignicola* Lindau, saprophytic on wood in water, and *R. operculatum* (De Wildeman) von Minden, probably saprophytic, on submerged surfaces of aquatic higher plants.

12. **Dangeardia** Schroder (*Ber. Deut. Bot. Gesell.*, **16**: 314, *pl. 20*, 1898).

Erected on a single species, *D. mamillata* Schroder, found on *Pandorina*.

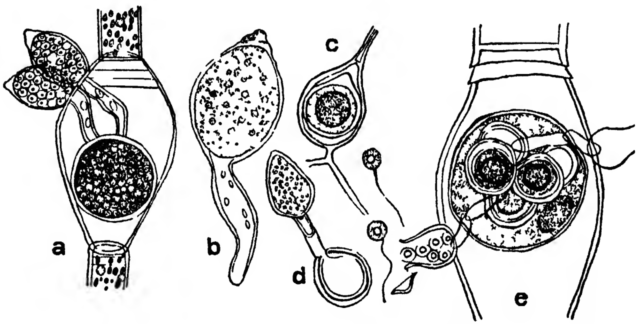

FIG 27—*Chytridium olla* Braun (*a*) Mature swarmsporangia attached to oospore of *Oedogonium* (*b*) Swarmsporangium enlarged (*c*) Resting spore (*d, e*) Germinating resting spores (*a, b, after A Braun 1855, c e after de Bary 1887*)

13. **Harpochytrium** Lagerheim (*Hedw.*, **29**: 142, 1890).

syn. *Fulminaria* Gobi, (*Scripta Hort. Bot. Petrop.*, **15**: 283, 1899;

Rhabdium Dangeard (*Ann. Mycol.*, **1**: 61, 1903).

A small but interesting genus embracing two or three species parasitic on algae (Fig. 26). These are thoroughly discussed and well illustrated by Atkinson (1903).

14. **Chytridium** A. Braun (Erscheinungen der Verjungung. p. 198, 1850; Berl. Akad. Abhandl., p. 23, *pl. 1*, 1855).

The oldest genus of the order. As here constituted it contains the type species, *C. olla* Braun (Fig. 27) and about six others of similar character, all occurring in algae.

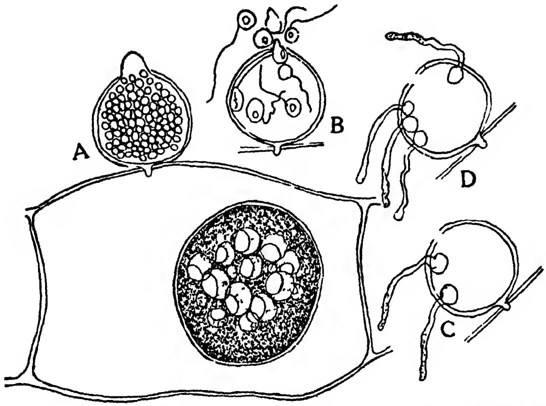

FIG. 28.—*Phlyctidium brevipes* (Atk.) v. Minden. *A.* Mature swarmsporangium crowded with swarmspores; inner layer of sporangial wall protruding as a papilla; rhizoids lacking. *B.* Swarmspores escaping. *C, D.* A few swarmspores germinating in the sporangium after failing to locate the exit pore. (*After Atkinson 1909.*)

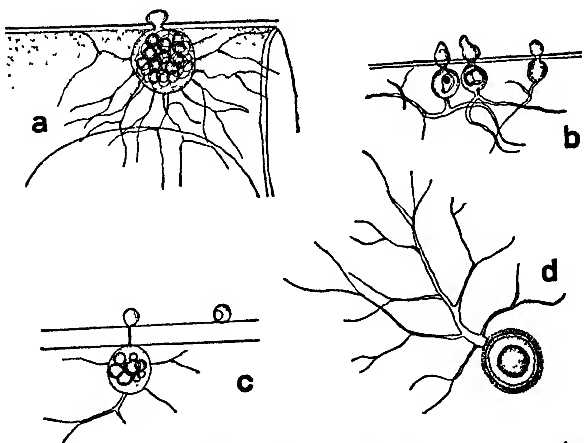

FIG. 29.—(*a, b*) *Entophlyctis bulligera* (Zopf) Fischer. (*c, d*) *Ent. confervae-glomeratae* (Cienkowski) Fischer. (*a*) Mature plant with papilla of dehiscence consisting of the membrane of the infecting swarmspore. (*b*) Young plants developing from infecting swarmspores. (*c*) Young plant with rhizoids developed from swarmspore; also an encysted swarmspore before germination. (*d*) Resting spore. (*After Zopf 1884.*)

15. Saccomyces Serbinow (*Scripta Hort Bot Petrop.*, **24**: 162, 1907)

Erected on a single species, *S. dangeardii* Serb, found in *Euglena* in Russia. See also *Rhizosiphon* Scherffel (1926 167)

16. Phlyctidium A. Braun (Monatsber d Akad. d Wiss 1855)

The genus contains several species, all of which occur in algae One of these *P brevipes* (Atk.) v. Minden (Fig 28) was first

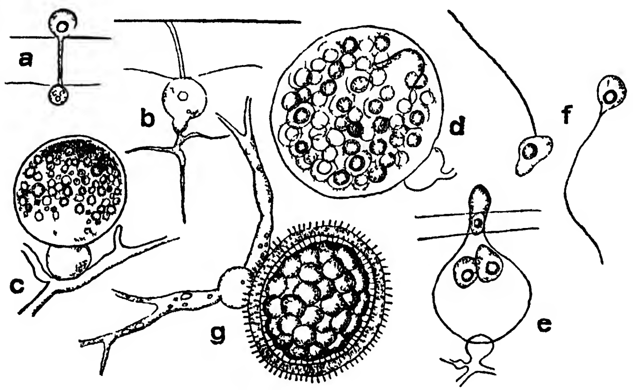

Fig 30 *Diplophlyctis intestina* (Schenk) Schroter (*a*) Infecting swarm spore (*b*) Young plant (*c*) Older plant with subsporangial vesicle (*d*) Mature plant with papilla of dehiscence (*e*) Sporangium freeing swarmspores (*f*) Swarmspores (*g*) Resting sporangium (*After Zopf 1884*)

described by Atkinson (1909 *a*) from North America on *Spirogyra* as *Rhizophidium brevipes* Atk Perhaps *Physorhizophidium* Scherffel (1926 181) belongs here.

17. Entophlyctis Fischer (1892 114).

The genus contains several species (Fig 29), all of which occur in algae A critical study of *E heliomorpha* has been made by Karling (1928)

18 **Diplophlyctis** Schroter (1892 78)

Erected on *D intestina* Schroter (Fig 30), found occurring in dead or dying cells of *Chara* and *Nitella* (consult Karling 1928 204).

19 Rhizophlyctis Fischer (1892 119)

The genus contains several species, all of which occur in algae (Fig 31)

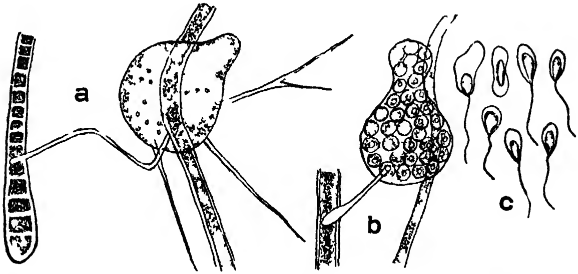

Fig 31 *Rhizophlyctis mastigotrichis* (Nowak) Fischer (*a*) Mature swarm sporangium with rhizoids attached to host threads (*b*) Same with swarm spores (*c*) Swarmspores (*After Nowakowski 1876*)

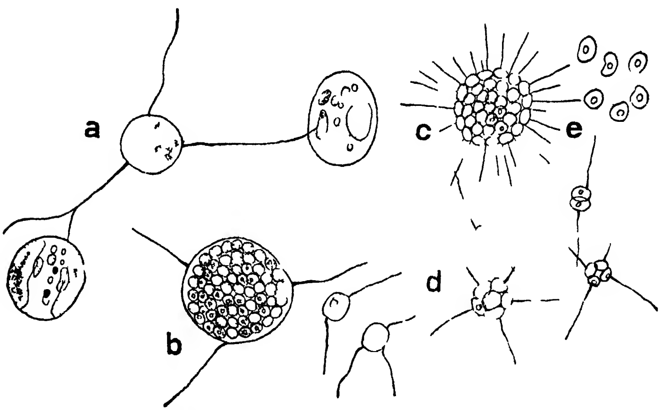

Fig 32—*Nowakowskia hormotheeae* Borzi on *Hormotheca sicula* (*a*) Plant sending rhizoids into several host cells (*b*) Mature swarm sporangium (*c*) Swarmspores in revealed mass after disintegration of sporangial wall (*d*) Swarm spore mass broken up into small colonies (*e*) Germinating swarmspores (*After Borzi 1885*)

20 Nowakowskia Borzi (*Bot Centralbl* **22** 23 *pl 1*, 1885)

This genus, based on *N hormotheeae* Borzi (Fig 32) on *Hormotheca sicula* in Sicily, is regarded as doubtful by Fischer (1892 122) It is essentially the same as *Rhizophlyctis* except in the

method of swarmspore discharge. In *Nowakowskia* according to Borzi the sporangial wall disintegrates leaving the swarmspores in a spherical *Volvox*-like mass which retains its form and rotates for a time, the spores finally separating from one another and swimming away.

21. **Sporophlyctis** Serbinow (*Scripta Bot. Hort. Univ. Petrop.*, **24**: 116, 164, 1907).

Erected on the single species, *S. rostrata* Serbinow, found on *Draparnaldia* in Russia. It has been collected also in America (Graff, 1928: 158).

22. **Polyphagus** Nowakowski (1876: 203).

Erected on the single species, *P. euglenae* Nowak., parasitic in *Euglena* and *Chlamydomonas*. The fungus is thoroughly discussed by Wager (1913), who outlines the sexual process as follows. Two cells, not differing morphologically from the vegetative cells, function as sex cells. The male cell, which is usually somewhat smaller than the female, puts out a slender pseudopodium-like process which comes in contact with the female cell and fuses with it. The zygote is formed in the tip of this tube, the contents of both male and female cells passing into it. A smooth or spiny wall is then formed on the zygote, and it assumes the spherical form of the mature resting spore.

Cladochytriaceae

The members of this family correspond with the Rhizidiaceae in the possession of a definite mycelium, but here it is widespreading and usually bears more than a single sporangium. Terminal and intercalary enlargements, formed throughout the mycelium, are transformed wholly or in part into sporangia or resting spores.

Key to Genera of Cladochytriaceae

I. Sporangiospores non-ciliate, amoeboid.

1. **Amoebochytrium**, p. 101

II. Sporangiospores ciliate.

A. Sporangia formed from enlargements of the mycelium, terminal or intercalary; resting spores rare or absent.

1. Sporangium opening by a lid, proliferating.

2. **Nowakowskiella**, p. 101

2. Sporangium lacking a lid and not proliferating
   a. Mycelium of rather broad, cylindrical threads; sporangia developed from fusiform enlargements of the hyphae and separated by short cylindrical cells.
      3. **Catenaria**, p. 101
   b. Mycelium of extremely delicate branching strands, developing globose or irregular enlargements which sometimes become septate into several cells; sporangium developed from an entire enlargement or from one of its cells; resting spores unknown.
      4. **Cladochytrium**, p. 102

B. Sporangia rarely formed, when present epibiotic and developing directly from the swarmspore; resting spores always present and abundant.
   1. Resting spore globose to ellipsoidal, usually not flattened on one side; parasite resulting in discoloration or slight thickening of the affected plant parts.
      5. **Physoderma**, p. 103
   2. Resting spore globose, but usually flattened to concave on one side; considerable deformation of affected portions of the host occurring.
      6. **Urophlyctis**, p. 107

1. **Amoebochytrium** Zopf (1884: 181).

Erected on the single species, *A. rhizidioides* Zopf, found in slime of *Chaetophora spp.*, but not in the cells, apparently known only from the original collection. Sporangium developed either from the spore or from an enlargement of the mycelium, flask-shaped with a long neck, described as freeing amoeboid non-ciliate spores. Resting spores unknown. It is possible that ciliate spores occur under certain conditions of environment.

2. **Nowakowskiella** Schröter (1892: 82).

Two species are included, *N. elegans* (Nowakowski) Schröter (Fig. 33) described from the slime of *Chaetophora* in Germany, and *N. ramosa* Butler (1907: 137) seen in decaying wheat culms in India. The former species has been found in America (Matthews, 1928).

3. **Catenaria** Sorokin (*Ann. Sci. Nat.* 6 ser. *bot.*, **4**: 67, 1876).

The genus includes the type species, *C. anguillulae* (Fig. 34) found in nematode and trematode worms, rotifer eggs, cysts of infusoria and *Nitella*, and *C. pygmaea* Serbinow a doubtful species in *Mougeotia*. The most recent and complete discussion of the genus is that of Butler (*Ann. Botany*, **42**: 813, 1928).

4. **Cladochytrium** Nowakowski (in Cohn, *Beitr. Biol. Pflanzen,* **2**: 92, 1877).

A thorough comparative study of this genus and the two following is greatly needed. The separation used here, adapted from von

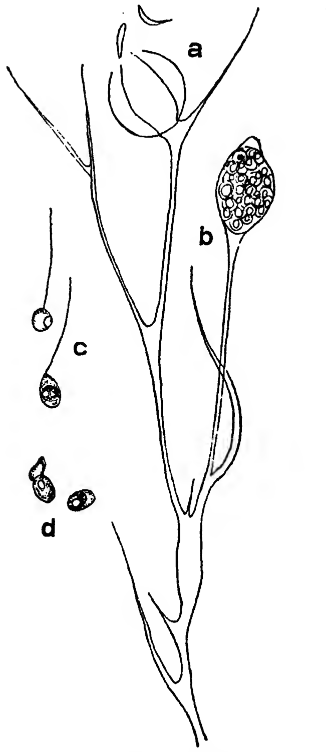

FIG. 33.—*Nowakowskiella elegans* (Nowak.) Schröter. (*a*) Terminal sporangium on branching mycelium; secondary sporangium formed by proliferation within the primary; lids of both fallen away. (*b*) Swarmsporangium containing spores. (*c*) Swarmspores. (*d*) Amoeboid zoospores. (*After* *Nowakowski* *1876*.)

Minden (1911: 389), is clearly inadequate, but can not be replaced by a more natural grouping until much additional work has been done. As here constituted the genus *Cladochytrium* contains relatively few species, and only one of these, the type species,

C. tenue Nowak. (Fig. 35), can be included with certainty. This species differs from those of *Physoderma* and *Urophlyctis* in its failure to form resting spores and in forming its sporangia from enlargements of the mycelium. It has been found in Europe in the tissues of various marsh plants (*Acorus*, *Iris*, etc.), and in

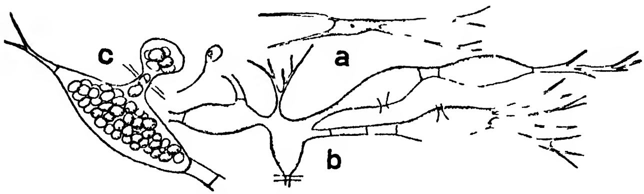

FIG 34.—*Catenaria anguillulae* Sorokin (*a*) Young thallus developed from swarmspore (*b*) Mature thallus with swarmsporangia and delicate terminal branches. (*c*) Swarmsporangium freeing swarmspores (*After Dangeard.*)

the slime which often covers their submerged surfaces. Other species doubtfully included in the genus are *C. polystomum* Zopf, *C cornutum* De Wildeman, and *C. irregulare* De Wildeman.

5. **Physoderma** Wallroth, (*Flora Crypt. Germ.*, 2: 192, 1833).

In this genus and in *Urophlyctis* all the species are parasitic in the tissues of higher plants. Resting spores are always present

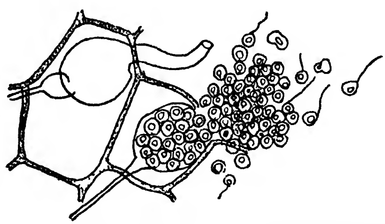

FIG. 35.—*Cladochytrium tenue* Nowakowski showing mycelium, swarmsporangia, and swarmspores. (*After Nowakowski 1876*)

and abundant. Sporangia have been found in only a few species, and when formed are epiphytic and develop directly from the swarmspore instead of from the mycelial enlargements. In these cases [*P. maculare* Wallr., *P. butomi* Schrot., *U. pulposa* (Wallr.) Schröt.], the mycelium attached to the sporangium is limited in extent, monophagus, and similar in appearance to that of *Rhizophidium* of the preceding family. Other swarmspores infecting

the host send their germ tubes into the interior and develop a wide-spreading mycelium having no connection with the sporangia. On this mycelium definite turbinate enlargements are formed (Fig. 37, *t*), which at maturity become septate, and from one of the cells of each enlargement a thick-walled resting spore develops. The other cells remain attached for a time, and in the literature bear the name "*Sammelzellen.*" The mycelium is very delicate, and soon disappears, the resting spores then lying free

FIG. 36.—*Urophlyctis alfalfae* (Lagerheim) Magnus, causing galls at the crown of an alfalfa plant. (*After Jones and Drechsler 1920.*)

in the host cells and giving no indication of their origin. They have been mistaken for the resting spores of *Synchytrium*, *e.g.*, *U. pluriannulatus* (B. & C.) Farlow (1908: 12). The details of resting spore formation are discussed by Clinton (1902: 56) for *P. maculare*, by Tisdale (1919: 147) for *P. zeae-maydis*, and by Jones and Drechsler (1920: 305) for *U. alfalfae* and *U. pluriannulatus*. From the latter account, especially it is evident that the development of the mycelium and resting spores is a very definite process. A comparison of the figures published by

Clinton and Drechsler shows, moreover, a striking similarity in morphology between species of the two genera The presence of the *Sammelzellen* on the resting spores of these forms was interpreted by Schroter as indicating a sexual conjugation of young thalli, and he erected the genus *Urophlyctis* to include the sexual forms This genus was incorporated by him in his family Oochytriaceae, while the forms in which indications of sexuality are absent were retained in *Physoderma* of the Cladochy-

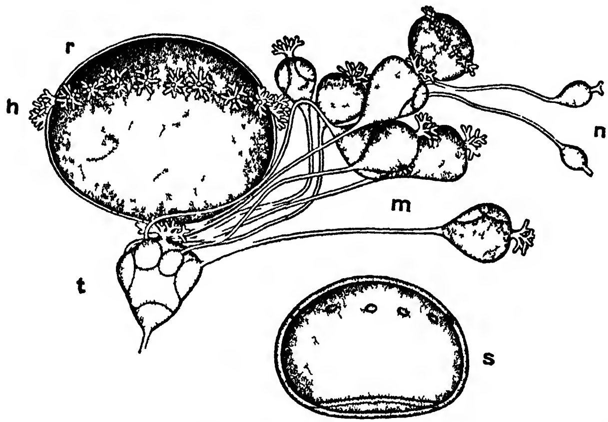

FIG 37 —*Urophlyctis pluriannulatus* (B & C) Farlow in *Sanicula* except (*s*) which is *U alfalfae* (Lagerheim) Magnus (*h*) Zone of haustoria (*m*) Secondary series of turbinate cells (*n*) Young turbinate cells of tertiary series (*r*) Mature resting spore which arose as a terminal expansion of the apical haustorium of turbinate cell ( ) Mature resting spore bearing zone of pits marking points of disappearance of haustoria (*t*) Septate turbinate cell whose cells have put out hyphae bearing apically a secondary series of turbinate cells (*After Jones and Drechsler 1920*)

triaceae His view was supported by investigations of Magnus (1897, 1901, 1902) but has not been confirmed by others There seems to be at present no reason for believing that a sexual process occurs in resting spore formation in any of the species Consequently, a new basis for separation of the genera *Physoderma* and *Urophlyctis* has been sought, the one used here being that suggested by von Minden As here constituted, the genus *Physoderma* includes those species which cause merely discoloration or slight thickening of the affected host parts while *Uro-*

phlyctis embraces those which cause pronounced deformation or gall formation. Correlated with this distinction there is a slight difference in the shape of the resting spore, that of *Urophlyctis* being more often and more strikingly flattened on one side. This separation is clearly inadequate and further investigation of these forms will probably result either in the fusion of the two genera or in a rearrangement of the species on a wholly new and as yet unsuspected basis.

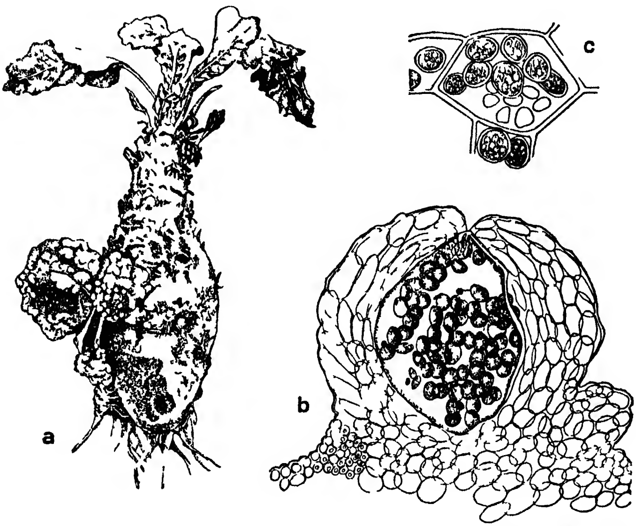

FIG 38.—(*a*) *Urophlyctis leproides* (Trabut) P Magnus forming galls on beet root (*b*) *U kriegeriana* Magnus, showing section through gall on *Carum* containing sorus of resting spores (*c*) *U pulposa* (Wallroth) Schroter, showing resting spores in cells of *Chenopodium* (*a, b, after Magnus, c, after Schröter 1897*)

The genus *Physoderma* as here constituted contains about twenty species, of which the following are known to occur in North America

P maculare Wallr —in *Alisma plantago*
P. menyanthis de Bary—in *Menyanthis trifoliata*
P zeae-maydis Shaw—in *Zea mays* (see *Mycologia*, **14** · 81, 1922)
P vagans Schroter—in *Sium*, etc
P heleocharidis Schroter—in *Eleocharis*

6. **Urophlyctis** Schröter (*Jahresber. Schles. Gesell. f. Vaterl. Cultur,* **60**: 198, 1882).

The present status of the genus *Urophlyctis* is indicated in the above discussion of *Physoderma.* Some of the species of the genus are limited to the underground portions of their host, while others occur only in the parts above ground. Some exert a dissolving action on the cells of the host and develop a wide-spreading mycelium; others are limited to the cells originally infected by the swarmspores. Eight species are included in the genus by von Minden. The following are known to occur in North America.

U. pulposa (Wallroth) Schröter (Fig. 38, *c*)—in *Atriplex* and *Chenopodium.*
U. alfalfae (Lagerheim) Magnus (Fig. 36, 37, *s*)—in *Medicago* (Wilson 1920).
U. pluriannulatus (B. & C.) Farlow (Fig. 37, *t*)—in *Sanicula.*
U. major Schröter—in *Rumex.*

Doubtful Chytridiales

1. **Hyphochytrium** Zopf (1884: 187).
syn. *Hyphophagus* v. Minden (1911: 420).

Those chytrids in which the mycelium is described as of considerable diameter were brought together in the family Hyphochytriaceae by Schröter (1892: 83). He included the genera *Catenaria, Hyphochytrium, Polyrhina,* and *Tetrachytrium.* Later von Minden (1911: 383) used the family name but excluded *Hyphochytrium,* the family as formed by him embracing *Macrochytrium, Zygochytrium,* and *Tetrachytrium.* There seems to be no sound basis for the recognition of the family and it is here discarded. The genus *Hyphochytrium* contains a single species, *H. infestans* Zopf (Fig. 39), parasitic in the apothecia of *Helotium.* The mycelium is rather broad, richly branched, of uniform diameter, and occasionally septate. Sporangia are formed from terminal or intercalary swellings. The swarmspores are uniciliate. Resting spores are unknown.

2. **Tetrachytrium** Sorokin (*Botan. Zeitung,* **32**: 307, 1874).

This genus, based on the single species, *T. triceps* Sorokin (Fig. 40), is known only from the original description and figures. It is included in the Hyphochytriaceae by Schröter (1892: 83) and von Minden (1911: 387).

3. **Zygochytrium** Sorokin (*Botan. Zeitung,* **32**: 305, 1874).

This genus, based on the single species, *Z. aurantiacum* Sorokin (Fig. 41), is known only from the original description

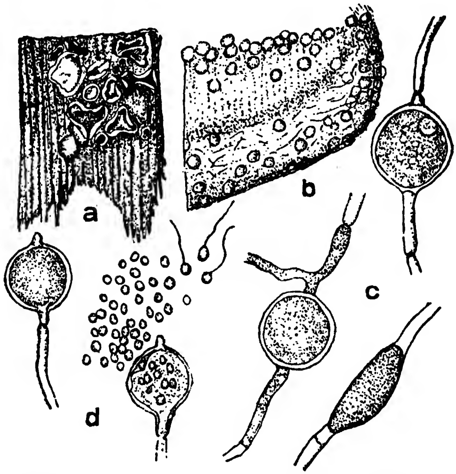

FIG. 39.—*Hypochytrium infestans* Zopf in apothecia of *Helotium*. (*a*) Apothecia. (*b*) Portion of apothecium in section showing swarmsporangia of the parasite. (*c*, *d*) Intercalary and terminal swarmsporangia. (*After Zopf 1884.*)

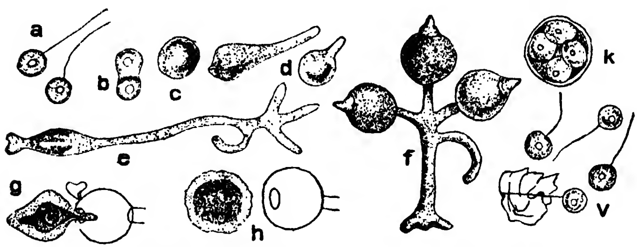

FIG. 40.—*Tetrachytrium triceps* Sorokin. (*a*) Swarmspores. (*b*) Conjugating gametes. (*c*) Zygote. (*d*) Germinating zygotes. (*e*) Immature plant. (*f*) Mature plant with haustorial disc. (*g*) Sporangium escaping from prosporangium; lid fallen away. (*h*) Free sporangium. (*k*) Sporangium with four swarmspores. (*v*) Escape of swarmspores. (*After Sorokin 1874.*)

and figures. If not founded on faulty observation it is an extremely interesting form, bearing uniciliate swarmspores in sporangia at the tips of a homothallic zygophore recalling that of *Sporodinia*.

4. **Macrochytrium** v. Minden (*Centralbl. f. Bakt.*, **8**: 824, 1902). (See also v. Minden, 1911: 385).

An interesting genus of doubtful relationships based on the single species, *M. botryoides* von Minden, found in Germany growing saprophytically on a submerged decaying apple. The

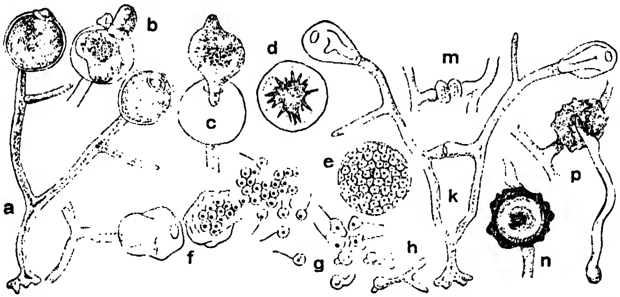

FIG. 41.—*Zygochytrium aurantiacum* Sorokin. (*a*) Mature plant bearing two prosporangia with papillate lids. (*b*, *c*) Sporangium emerging from pore after turning aside of lid. (*d*) Free sporangium. (*e*) Sporangium containing swarmspores. (*f*, *g*, *h*) Swarmspores escaping, becoming amoeboid, and germinating. (*k*, *m*) Conjugation of gametic branches. (*n*) Mature zygospore. (*p*) Zygospore germination. (*After Sorokin* 1874.)

mycelium is cylindrical and broader than in other members of the order. Superficially the fungus resembles *Rhizophidium* except in its much greater size. The sporangium dehisces by a large lid. Resting spores are unknown.

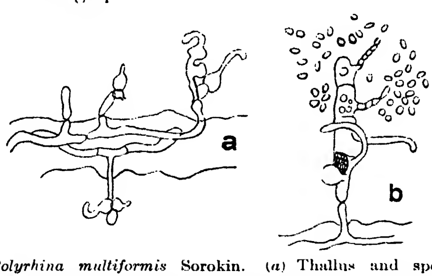

FIG. 42.—*Polyrhina multiformis* Sorokin. (*a*) Thallus and sporangia. (*b*) Mature swarmsporangia with escaping swarmspores. (*After Sorokin.*)

5. **Rhodochytrium** Lagerheim (*Botan. Zeitung*, **51**: 43, 1893).

The genus *Rhodochytrium*, based on *R. spilanthidis* Lag. parasitic on the common ragweed, *Ambrosia*, is of extreme interest to the student of phylogeny. The organism is evidently an

alga, stores starch, and is most closely related to another algal genus, *Phyllobium* Klebs (*Bot. Zeit.*, **39**: 249, 1881). Its parasitic habit and its lack of chlorophyll nevertheless indicate fungous tendencies. The life history and cytology of the species are discussed by Griggs (1912), Atkinson (1908 *a*, *b*), and Ramsbottom (1913). In gross aspect the organism resembles *Synchytrium* (see p. 13).

6. **Mitochytridium** Dangeard.

See discussion under Ancylistales.

7. **Polyrhina** Sorokin.

The single species, *P. multiformis* Sorokin (Fig. 42), is apparently the same as *Harposporium anguillulae* Lohde (see Zopf, 1888, for good figures). Its position is doubtful.

8. **Rhizidiocystis** Sideris (*Phytopathology*, **19**: 376, 1929).

Based on *R. ananasi* Sideris, parasitic in root hairs of pineapple. Placed by the author in the Cladochytriaceae.

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CHAPTER IV

ANCYLISTALES

The members of this order are all endobiotic parasites, the thallus in most cases being confined to a single host cell. The parasite gains entrance to the host by means of a delicate infection tube, which on reaching the interior rounds up at the tip to form a small spherical bladder. This bladder by further growth develops into the thallus. The young thallus is a rather short, unicellular, more or less cylindrical tube. In some species it is somewhat branched or lobed. At maturity, it is usually divided by transverse septa into a number of cells. The component cells of the thallus may function variously, some as sporangia, some as gametangia, and some vegetatively. In the last case the cell germinates directly by a slender germ tube, which may become much elongated and serve as an infection thread by means of which the fungus enters another host cell. The cell of the thallus in this case is perhaps to be regarded properly as a sporangium which has assumed the method of germination characteristic of this structure in the higher Oomycetes. This type of germination is relatively rare in the order, the sporangia in most species forming swarmspores. In some cases all the cells of a single thallus function alike. Sporangia and sexual cells are developed in the same or different thalli, a given species being usually either homothallic or heterothallic.

The sexual process in the group has not yet been adequately studied. The cells of the thallus which function as male and female gametangia respectively show a relatively slight degree of morphological differentiation as compared with those of the Oomycetes. The female is typically larger and more characteristically barrel-shaped than the male which is commonly cylindrical. Usually copulation of the two cells is accomplished by means of a more or less elongate conjugation tube. The terms oogonium and antheridium may be used only tentatively since oosphere formation has not been convincingly demonstrated. In *Ancylistes* the oosphere seems to be clearly absent. If present in other members of the group it is at best imperfectly differ-

entiated. Nevertheless, the resting spore at maturity lies free in the female cell and resembles the oospore of the Saprolegniales. The sexual process has been studied cytologically in only two species, *Myzocytium vermicolum* Zopf and *Ancylistes closterii* Pfitzer. The nuclear history in these forms is described by Dangeard, and his results are discussed under these genera below. Other cytological investigations are urgently needed, since at present, the fundamental nature of the sexual process in the various members of the group is in doubt. Not infrequently resting spores are formed apparently parthenogenetically from the contents of a single cell. The resting spore in all cases is spherical and thick-walled. In some species it germinates by swarmspores, in others by a germ tube.

In several respects the members of the order seem to be more highly developed than the Chytridiales. The resting spore lies free in the female gametangium, a conjugation tube, rare in the chytrids, is commonly formed, and in *Ancylistes* both the sporangium and resting spore germinate by germ tube. The cells composing the thallus show, moreover, a greater ability to function in diverse capacities, division of labor comparable to that in higher groups being evident. In these various respects the group appears to approach the Saprolegniales and is perhaps to be regarded as intermediate in type between that order and the Chytridiales. The group is regarded as more primitive than the Saprolegniales in that mycelium is absent or poorly developed, a well defined oosphere absent, and the gametangia not clearly differentiated as oogonium and antheridium. In Ancylistes, particularly, zygomycetous features are evident.

The order, as here treated, contains the single family Ancylistaceae.

Key to Genera of Ancylistales

I. Asexual reproduction accomplished by swarmspores freed from sporangia.

A. Mature thallus an unbranched tube, divided by transverse septa into a row of cells of similar size and form, usually constricted at the septa.

1. Swarmspores escaping from the sporangium fully formed, and encysting individually at its mouth as in *Achlya*.

1. Achlyogeton, p. 119

2. Swarmspores not encysting at the mouth of the sporangium; contents of sporangium usually extruded into a vesicle.

2. Myzocytium, p. 120

B. Mature thallus more or less branched, transversely septate, but not markedly constricted at the septa; component cells often differing considerably in size and form.

II. Swarmspores not formed; asexual cells of thallus germinating by germ tubes; thallus sometimes considerably branched.

1. **Achlyogeton** Schenk (1859).

In this genus the mature thallus is an unbranched elongate tube, septate at regular intervals, and constricted so deeply at the septa that a row of broadly ellipsoidal, slightly connected cells results. Each cell functions as a sporangium, the swarmspores passing through an exit tube to the exterior of the host cell. At the rupture of the tip of the tube the swarmspores pass out and encyst individually at the mouth, forming a globose aggregation of tiny spheres as in *Achlya*. After encystment they swim away. They were figured as uniciliate by Schenk, but

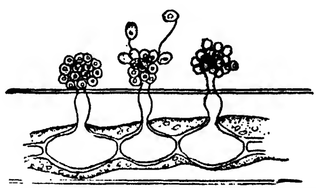

FIG. 43.—*Achlyogeton entophytum* Schenk, in thread of *Cladophora*. Chain of segments functioning as sporangia. (*After Schenk 1859.*)

inasmuch as the swarmspores in all the other accepted members of the order (see *Resticularia*) are biciliate the point requires verification. No indication of sexuality has been obtained. Martin (1927) figures thick-walled resting spores which he found associated with the sporangia but fails to demonstrate their true nature. Oospore-like resting spores, such as occur in other genera of the family, are unknown.

The genus was based on a single species, *A. entophytum* Schenk (Fig. 43), found in cells of *Cladophora*. It was recently rediscovered by Martin (1927) in Iowa. Another species found in the bodies of Anguillulidae, and referred to this genus by Sorokin as *A. rostratum* is imperfectly known, and may be more properly included in or near *Myzocytium vermicolum* (Zopf) Fischer, found in the same host.

2. **Myzocytium** Schenk (Über das Vorkommen Kontraktiler Zellen in Pflanzenreich, p. 70, 1858).

The mature thallus in this genus corresponds rather closely in form with that of *Achlyogeton*, consisting, as there, of a simple unbranched tube. Transverse septation results in the formation of a row of more or less bead-like cells, as many as ten being formed in a single thallus. Rarely reduced non-septate thalli

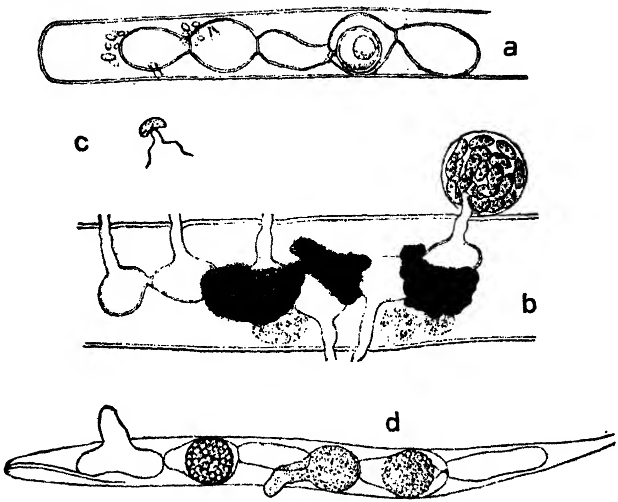

FIG. 44.—(*a–c*) *Myzocytium proliferum* Schenk in *Spirogyra*. (*a*) Different cells of a single thallus functioning as sporangia and sex cells. (*b*) Chain of sporangia. (*c*) Swarmspore. (*d*) *My. vermicolum* (Zopf) Fischer in *Anguillula*. (*After Zopf 1884*.)

occur which may be easily confused with those of *Olpidium*. A reduced two-celled thallus was misunderstood by Sorokin, and made the basis of his genus *Bicricium*. The cells of the thallus in *Myzocytium* function either as sporangia or sexual cells. In the latter case contiguous cells of the thallus usually function as oogonium and antheridium, since the species are almost exclusively homothallic. Following fertilization a spherical thick-walled resting spore ("oospore") is formed, and at maturity lies free in the oogonium. After hibernation it germinates by

swarmspores. Sporangia and sexual cells are formed in the same or different thalli. The germinating sporangium puts out a slender exit tube as in *Achlyogeton,* but here a thin-walled vesicle rounds up at the tip of the tube and the contents of the sporangium pass into it. In *M. proliferum* Schenk (Fig. 44, *b*) the process of swarmspore delimitation is completed in the vesicle, the swarmspores being no more than imperfectly fashioned when the protoplasm flows through the tube. In *M. vermicolum* (Zopf) Fischer (Fig. 44, *d*), the swarmspores are fully formed in the sporangium, and the vesicle may rupture before all of the swarmspores have passed into it (Dangeard, 1906: *pl. 3*). In any case there is no *Achlya*-like encystment comparable to that occurring in *Achlyogeton.*

The cells of the thallus which function as sporangia are globose, ellipsoidal, or irregularly contoured. Rarely two exit tubes occur. The swarmspores are laterally biciliate, the cilium which trails in swimming being longer than that which precedes the spore. The gametangia resemble the sporangia in shape, the male cell being commonly the more slender.

Knowledge of nuclear phenomena in the genus rests on the work of Dangeard (1906) on *M. vermicolum* Zopf. Numerous nuclei lie scattered through the young thallus. Each sporangium receives several nuclei when segmentation of the thallus occurs, and subsequently these divide repeatedly to provide the nuclei for the uninucleate swarmspores. In those cells of the thallus which are to function as gametangia a relatively small number of nuclei exist. The male gametangium ("antheridum") usually contains two nuclei, while the female gametangium ("oogonium") contains approximately eight. Later all but one of the female nuclei disintegrate and disappear. One male nucleus enters the female gametangium, while the other usually fails to function. In cases in which the male cell is intercalary between two female cells it is possible that the two male nuclei fertilize different female cells. A coenocentrum was not demonstrated. The sexual nuclei fuse in the young resting spore. After hibernation the fusion nucleus divides, about ten nuclei being provided for the swarmspores.

The genus was founded on *M. proliferum* Schenk, occurring in the cells of various green algae (*Oedogonium, Cladophora, Zygnema, Spirogyra, Mesocarpus, Mougeotia*). This species is widely distributed in Europe and has been collected in America (Martin

1927; Graff 1928). The following additional species have been referred to the genus.

M. megastomum De Wildeman—in *Closterium* and *Spirotaenia*.
M. vermicolum (Zopf) Fischer—in *Anguillulidae*.
M. (?) *irregulare* Petersen (perhaps a species of *Lagenidium*)—in *Cosmarium* and *Micrasterias*.

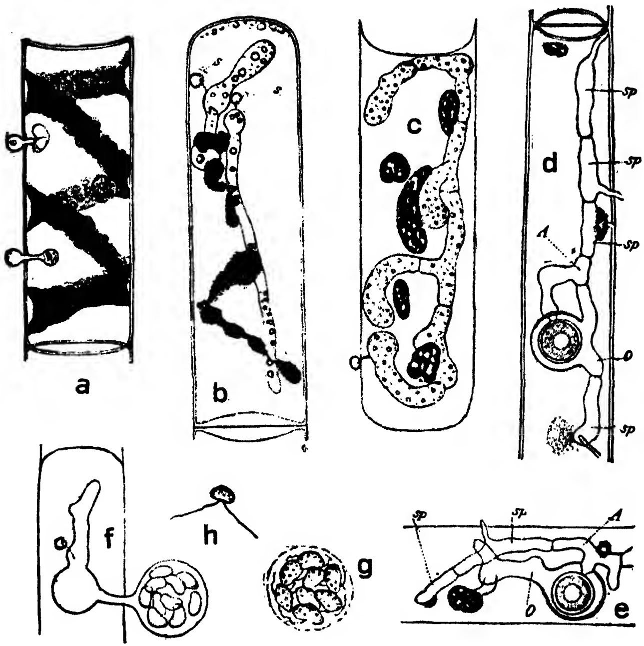

FIG. 45.—*Lagenidium rabenhorstii* Zopf in vegetative cells of *Spirogyra*. (*a*) Infecting swarmspores. (*b*) Young non-septate thallus developed from swarmspore. (*c*) Septate thallus. (*d, e*) Cells of thallus functioning as sporangia (sp.), antheridia (A), and oogonia (O). (*f–h*) Swarmspore formation. (*After Zopf 1884.*)

3. **Lagenidium** Schenk (*Verhandl. Phys. Med. Gesell. Würzburg,* 9: 27, 1857).

The mature thallus in *Lagenidium* is an irregular tube, more or less branched or provided with protuberances. Septa divide the thallus at indefinite intervals into cells, but prominent con-

strictions at the septa are usually not present. The resulting cells differ in size and form, and some of them may be slightly branched. As in *Myzocytium* the component cells of the thallus may function either as sporangia or sexual cells, but here the male and female gametangia may occur on the same or on different thalli. In some species (*e.g.*, *L. entophytum*) male cells are not differentiated, the "oospores" being developed without fertilization (parthenogenetically). The germination of these spores has not yet been observed. The classical figures of Zopf (1884: *pl. 1–3*) picture the various steps in the life cycle in two species of the genus. According to his account and those of other early students the sporangium germinates by the emission of

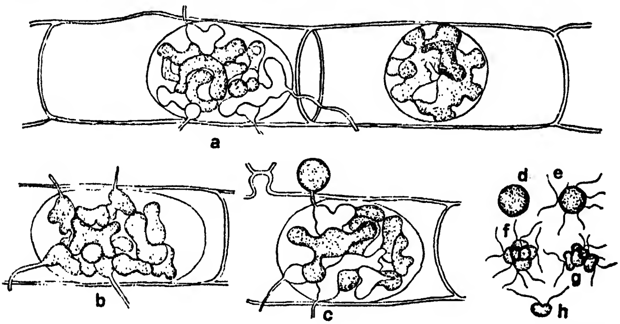

FIG. 46.—*Lagenidium americanum* Atkinson in zygospores of *Spirogyra*. (*a*, *b*) Sporangia, some emptied. (*c–h*) Stages in swarmspore formation. (*After Atkinson 1909.*)

the contents into a bladder at the mouth of the exit tube, the swarmspores being delimited in the bladder. Atkinson (1909: 330) after studying two species, including one of those figured by Zopf, states that, in fact, a bladder is not formed. According to his account the protoplasm escapes from the tip of the tube as a naked mass and though usually remaining at the mouth in the form of a ball sometimes breaks away as a detached sphere. In a few moments a rotary motion begins, and the swarmspores are gradually delimited and escape one by one from the moving mass. The details of the process are described at some length and in an interesting manner. To the writer it seems likely that the bladder is sometimes present and that at other times the tip of the exit tube ruptures before it forms. It would seem that too much emphasis has been placed on the

taxonomic importance of the presence or absence of the vesicle here and elsewhere in the Phycomycetes.

The genus is the largest in the order, the following species being included by von Minden (1911). More recently still other species have been described (Scherffel 1925).

L. rabenhorstii Zopf (Fig. 45)—in vegetative cells of *Spirogyra, Mougeotia,* and *Mesocarpus.*

L. entophytum (Pringsheim) Zopf—in the zygospore of *Spirogyra,* often filling it, but not found in the vegetative cells. The species *L. americanum* Atkinson (Fig. 46) occurring in the same location is perhaps the same species.

L. gracile Zopf—also in the zygospore of *Spirogyra.* This species has a more slender, less branched thallus than the preceding. "Antheridia" are absent in both.

L. enecans Zopf—in diatoms.

L. pygmaeum Zopf—in pollen grains.

L. ellipticum De Wildeman—An imperfectly known and doubtful form occurring in rhizoids of mosses.

L. intermedium De Wildeman—in *Closterium.*

L. closterii De Wildeman—in *Closterium.*

L. syncytiorum Klebahn—in *Oedogonium.*

L. marchelianum De Wildeman—in *Oedogonium.*

4. **Ancylistes** Pfitzer (1872).

The young thallus in this genus is a cylindrical tube, and may be somewhat branched. At maturity it becomes septate at rather regular intervals. The resultant cells may swell slightly, but deep constriction at the septa is not usual. Several thalli may lie parallel in the host cell. Swarmspores are not formed in the genus, and typical sporangia are lacking. The cells of the thallus function either as sexual cells or vegetative cells. In the latter case a slender germ tube arises from the cell, passes through the wall of the host cell, and elongates into a mycelial thread. This comes in contact with another host cell, bends around it, penetrates it by means of a delicate infection tube, and discharges its contents through this into a thin-walled bladder which forms at the inner end of the tube. This bladder then develops into a new thallus. The cells which develop vegetatively in this manner are clearly homologous with the sporangia of related genera, but they never form endogenous spores. They have merely assumed the method of germination usual in higher Oomycetes.

The genus was founded on a single species, *A. closterii* Pfitzer (Fig. 47), occurring in the desmid *Closterium.* In this species

all the cells of a single thallus function alike, as vegetative cells, as male cells, or as female cells. This species is consequently heterothallic, two thalli lying side by side functioning as male and female thalli respectively, and all the resting spores being formed in one thallus. The male gametangium puts out a short fertilization tube which fuses with the wall of the nearest female cell and the content of the male cell then passes over. A definite oosphere has not been demonstrated, but the contents of the

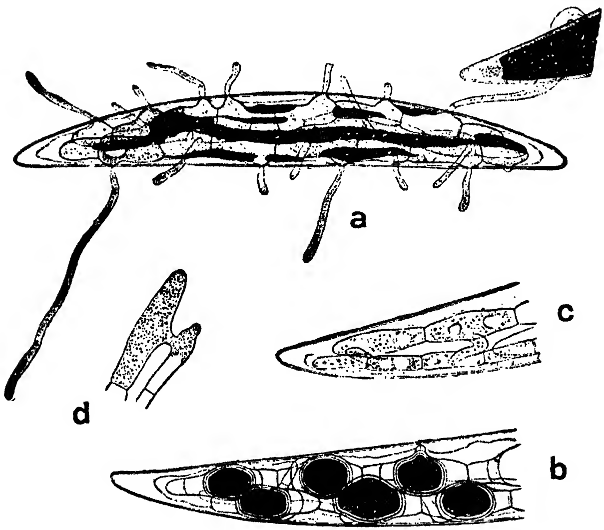

FIG. 47.—*Ancylistes closterii* Pfitzer in cells of *Closterium*. (*a*) Cells of thallus germinating to form infection threads. (*b*) Oospores. (*c*, *d*) Cells of neighboring thalli united by conjugation tubes preceding oospore formation. (*After Pfitzer 1872.*)

fertilized cell contract to form an oospore-like resting spore. Germination of the spore is by germ tube. Another species, *A. pfeifferi* de Beck, also occurring in *Closterium*, has been incorporated in the genus but is imperfectly understood. In it the male and female gametangia appear to alternate in the same thallus, but this has not been clearly demonstrated. Some thalli function vegetatively as in the above species. The method of resting spore germination is unknown. The absence of swarmspores gives the genus particular interest, and the formation of

germ tubes marks it as the most highly developed member of the order.

Knowledge of the nuclear history in the genus rests wholly on the work of Dangeard (1906) on *A. closterii* Pfitzer. He pictures the young thallus as plurinucleate, the nuclei being regularly spaced in a single row in the thread. In the segmentation of the thallus each cell receives several nuclei. In the beginning, each vegetative cell contains four or five nuclei, but the number is doubled by a single simultaneous mitosis. The eight or ten resultant nuclei pass over with the cytoplasm through the germ tube and infection thread into the new host cell. The male gametangium at first usually contains two nuclei while the female possesses six or eight. A single simultaneous division later doubles the number in each. The nuclei and cytoplasm of the male cell enter the female, but nuclear fusion apparently fails to occur. The resting spore matures in the plurinucleate condition, containing both male and female nuclei. It is possible that a fusion occurs at the time of germination, though it has not been seen. Germination is by tube (Dangeard, 1886).

Doubtful or Excluded Genera

1. **Resticularia** Dangeard (*Le Botaniste*, **2**: 96, *pl. 4*, 1891).

This genus was based on a single species, *R. nodosa* Dang. (Fig. 48), found parasitic in *Lyngbya*. It was accepted by Fischer (1892: 84) and Schröter (1893: 92), both authors placing it next to Ancylistes. Later this species was discovered by Fritsch (1903: 649) in England growing in *Tolypothrix*, and was redescribed by him. He states that it occasionally forms sporangia containing uniciliate swarmspores. He also described as new another species, *R. boodlei* Fritsch, found in the same host. The genus is listed by von Minden (1911: 444) as a doubtful member of the Ancylistales. In the present state of our knowledge a satisfactory disposition of it cannot be made.

2. **Rhizomyxa** Borzi.

Discussed above under *Sorosphaera* of the Plasmodiophoraceae.

3. **Lagenidiopsis** De Wildeman (*Ann. Soc. Belge Micros.*, **20**: 109, 1896).

A single imperfectly understood species, *L. reducta* De Wild., found in oogonia of Characeae.

4. **Mitochytrium** Dangeard (1911: 200).

This genus was erected on the single species, *M. ramosum* Dang., found in the cells of *Docidium*, a desmid. The thallus, as figured, resembles that of *Lagenidium* except that it is provided at several points with finely branched rhizoids and is non-septate. The form was inadequately discussed, but was regarded by Dangeard as intermediate between the Ancylistales and Chytridiales.

5. **Protascus** Dangeard (1906), not *Protascus* Wolk (1913).

This is a monotypic genus based on the single species, *P. subuliformis* Dang., parasitic in the body of Anguillulidae. The

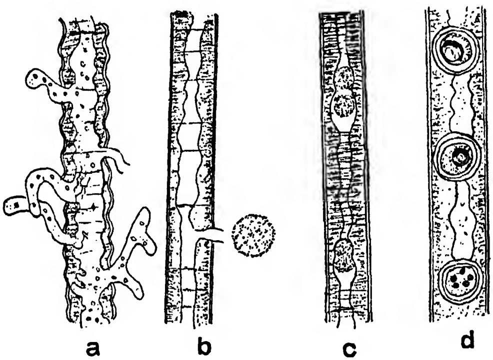

FIG. 48.—*Resticularia nodosa* Dangeard in *Lyngbya*. (*a*) Thallus sending branches outside of host. (*b*) Sporangium germinating. (*c,d*) Zygospore formation. (*After Dangeard 1890.*)

fungus resembles in general structure *Myzocytium* and *Lagenidium* but differs in several striking respects. The endozoic thallus is septate at maturity into eight cells of similar aspect. These fall apart at the septa, and may be termed segments. They function as sporangia or gametangia. The number of spores in the sporangium is extremely variable (approx. 8–200). They pass through an exit tube to the surface of the host, and are there apparently discharged with considerable violence. The spore is non-motile and in form is clavate with the narrow end tapering to a sharp point. Infection is accomplished when the narrowed end of the spore attaches itself to the new host. Segments functioning as sporangia and gametangia may result from

a single thallus, but conjugating segments arise from different thalli. As a result of conjugation a spherical "oospore" is formed in one segment of each pair.

The species has been studied by Dangeard (1906) and Maupas (1915). The former author saw it only in the sporangial stage, and regarded it as one of the Hemiascales. The reasons for incorporating the genus in the Ancylistales are discussed by Maire (1915). He suggests that the fungus be made the basis of a new family, Protascaceae, which he regards as intermediate between the Lagenidiaceae and Ancylistaceae. The erection of the new family seems premature in the light of our incomplete knowledge of the order, while the small size of the group makes it unnecessary. The name, Protascaceae, is unfortunate, in that the group may easily be confused with the Protascales of the Ascomycetes.

The writer is not convinced that *Protascus* is closely related to the other genera incorporated in the Ancylistales, and its inclusion here is at best tentative. At present, no more satisfactory disposition of it seems possible.

6. **Lagena** Vanterpool & Ledingham (1930: 192).

A monotypic genus, recently erected on *L. radicicola* Vanterpool & Ledingham, an obligate parasite in rootlets of cereals in Saskatchewan. Mycelium is absent. The thallus is unicellular, unbranched, ovoid to cylindrical, sometimes curved, and is attached to the host wall by a neck. It may function as a sporangium or "coenogametangium." The contents of the sporangium escape into a thin-walled vesicle, in which bean-shaped, laterally biciliate swarmspores are formed. Thalli functioning as "coenogametangia" conjugate in pairs by means of a tube, and a thick-walled "oospore" recalling that of *Pythium* is formed. Apparently the genus lies near *Lagenidium.*

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CHAPTER V

BLASTOCLADIALES

This small order consists of the single family Blastocladiaceae embracing about a dozen species in three genera. The forms included agree in the possession of non-cellulose walls and uniciliate swarmspores. The group is apparently most closely related to the Monoblepharidales. It has been given ordinal rank previously by Petersen (1910: 494) and von Minden (1916: 189). Other authors have incorporated its genera in the Saprolegniales. The recent monograph of Kanouse (1927: 295) is the best general treatment of the group. The members of the order are typically aquatic. They occur as saprophytes on submerged plant and animal substrata. In recent years a few species have been isolated from the soil (Coker and Braxton, 1926: 146; Harvey, 1925: 162; 1928: 560). Of the three genera included, *Blastocladia* and *Allomyces* are clearly very closely related. The third, *Gonapodya*, is somewhat less certainly a member of the group.

In *Blastocladia* and *Allomyces* the thallus is differentiated into a main thickened axis or trunk and slender branches, and is attached to the substratum by branching rhizoids. In these respects, relationship is indicated to both the Monoblepharidales and the Leptomitaceae of the Saprolegniales. The similarity to genera such as *Araiospora* and *Rhipidium* of the latter group is pronounced. In *Gonapodya* there is no differentiation of the thallus into a central thickened portion and slender branches, and rhizoids are lacking. The thallus is composed of cylindrical hyphae which are definitely and often frequently constricted as in the Leptomitaceae, and cellulin plugs lie in the constrictions.

Asexual reproduction takes place by means of swarmspores borne in thin-walled sporangia or in peculiar thick-walled resting sporangia. The thin-walled sporangium varies in shape from ovoid to linear, and at maturity is provided with a single apical exit papilla or with several scattered over its surface. The sporangium is developed terminally, but further growth of the

hypha may cause it to assume a lateral position. Less often sporangia are cut off in basipetal succession, and form a chain (Coker and Braxton, 1926: *pl. 10*). The swarmspores are monoplanetic. In some cases they pass into a vesicle as in *Pythium* before being freed. In *Gonapodya* repeated proliferation of new sporangia within the old occurs.

The resting sporangium is an outstanding feature of the morphology of *Blastocladia* and *Allomyces*, but is absent in *Gonapodya*. It corresponds more or less in form, size, and position with the thin-walled sporangium, but is clearly very different in character. It is thick-walled, the wall being composed of three layers, a middle thick layer and outer and inner thin ones. The outer layer is in reality the original wall of the hyphal cell, and in some species at the maturity of the resting sporangium this outer wall splits allowing the sporangium, enclosed in the other two walls, to fall away. In other cases the outer wall remains in close contact with the sporangium and is carried away with it. The appearance of the mature resting sporangium is characteristic. In no other known group of Phycomycetes is there a similar structure. Its surface is covered with minute dots, which are shown in section to be the mouths of cylindric tubes lying in the middle wall and almost traversing it. At germination this wall cracks open, and a prominent exit papilla is formed on the inner, the escaping swarmspores resembling those freed by the thin-walled sporangium.

Various names have been applied by different writers to this resting sporangium. It has been termed the conidium, the resting spore, and the resting cell. Butler (1911: 1030) suggests that it is perhaps a parthenogenetic oospore. Kanouse (1927: 292) uses the terms oogonium and oospore in this connection without qualification. Moreover, she describes and figures for *Blastocladia globosa* Kanouse, slender filaments associated with the resting sporangium which, she says, are undoubtedly antheridial branches. In a single case, she found a cell cut off at the tip of a branch by a definite septum, and regards this as an antheridium. The process of fertilization was not observed, nor, in fact, any indication given as to how it may be effected. She suggests the possibility that it is accomplished by means of motile male cells, though none were observed. She admits that, in any case, these so-called "antheridia" are rare, and that the "oospores" (parthenospores) usually mature parthenogenetically.

The true nature of the sexual process in the group has been only very recently elucidated by Kniep (1929). Working with a hitherto undescribed species, *Allomyces javanicus* Kniep, he has discovered a sexual process of so unique and distinctive a type that on this basis alone the group is deserving of ordinal rank. In this species the usual thin-walled sporangia and the thick-walled resting sporangia occur, but in addition to these, thin-walled sexual organs (gametangia) resembling the sporangia in shape are produced. The male and female organs, though similar in shape, differ regularly in size. In both of them uniciliate swarm cells termed gametes are formed. The larger gametangium is regarded by Kniep as the female. The gametes delimited in it are markedly larger than those formed in the smaller male gametangium. After their escape from the gametangia the larger and smaller gametes fuse in pairs forming biciliate zygotes. The zygote swims for a time, but finally comes to rest, assumes a membrane, and puts out a germ tube which develops directly into the rhizoid system which is to anchor the new plant. Kniep applies the terms antheridium and oogonium to the smaller and larger sexual organs respectively.

Fusion of ciliate gametes in pairs is not known to occur elsewhere in the Phycomycetes above the level of the Chytridiales. There it has been observed in several species of *Olpidium* and *Synchytrium*. In the Monoblepharidales the male gametangium frees wholly similar ciliate cells, but the content of the female gametangium rounds up to form a non-ciliate practically non-motile oosphere. As the Monoblepharidales and Blastocladiales are admittedly closely related the discovery in other species of these groups of intermediate types of sexuality would not be surprising. Since, at present, the sexual process in other species of the Blastocladiales is wholly unknown the acceptance of heterogamic copulation of planogametes as the typical method of sexuality in the group must be regarded as tentative.

As Kniep finds the thick-walled resting sporangia also in *Allomyces javanicus* these structures are apparently of the nature of chlamydospores and are hardly to be regarded as parthenogenetically developed oospores.

Though the swarmspore is typically uniciliate throughout the order, occasional individuals with two or more cilia are observed. Kniep has shown that these represent merely cases

in which the final cleavage of the cytoplasm of the sporangium has failed to occur. Such swarmspores have two or more nuclei.

Key to Genera of Blastocladiaceae

I. Thallus not differentiated into a stout main axis and more slender branches, composed of cylindrical hyphae which are definitely and usually frequently constricted; sporangia proliferating; thick-walled resting sporangia unknown.

1. Gonapodya, p. 134

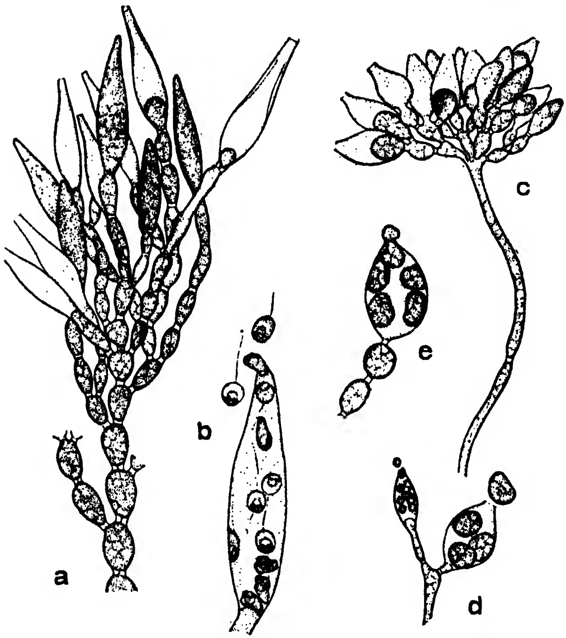

FIG. 49.—(*a, b*) *Gonapodya siliquaeformis* (Reinsch) Thaxter. (*c–e*) *G. polymorpha* Thaxter. (*a*) Typical plant, segments short, sporangia proliferating. (*b*) Sporangium freeing uniciliate swarmspores. (*c*) Segmented portions of plant borne sub-umbellately on a slender hypha. (*d, e*) Sporangia showing extreme variation in size of swarmspores. (*After Thaxter 1895.*)

II. Thallus provided with a stout main axis bearing more slender branches; thick-walled resting sporangia present.

A. Thallus separated into definite segments by pseudosepta, sometimes slightly constricted at the septa.

2. Allomyces, p. 135

B. Thallus lacking pseudosepta, not definitely constricted.
3. Blastocladia, p. 136

1. **Gonapodya** Fischer (1892: 378).

A small genus of two species, *G. siliquaeformis* (Reinsch) Thaxter and *G. polymorpha* Thaxter. The genus is of somewhat doubtful affinities, and is placed here chiefly on account of its uniciliate zoospores and non-cellullose walls. In its prominently segmented mycelium it corresponds to the members of the Leptomitaceae of the Saprolegniales. Since the species are known only in the sporangial condition and lack the peculiar resting sporangia of *Blastocladia* and *Allomyces*, the incorporation of the genus here is at best tentative.

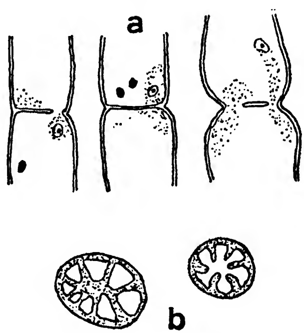

FIG. 50.—*Allomyces arbuscula* Butler. (*a*) Pseudosepta as seen in longitudinal section. (*b*) Same in transverse section. (*After Barrett 1912.*)

The thallus is filamentous, resembling somewhat that of *Leptomitus*, but with shorter segments (Fig. 49). A basal portion attached to the substratum by rhizoids is lacking. The hyphae are usually deeply constricted, so much so that at times the short rounded segments give the aspect of a chain of beads. Branching occurs chiefly at the tips of the primary hyphae, dense tufts of segmented branchlets terminating slender more or less unsegmented threads. The sporangia are borne terminally, and undergo repeated proliferation. They are elongated and taper toward the tip. The zoospores are typically uniciliate, though biciliate spores apparently sometimes exist.

The species occur on submerged fruits, twigs, and other plant parts and are saprophytic.

2. **Allomyces** Butler (1911: 1027).

syn. *Septocladia* Coker & Grant (1922: 180).

The thallus is differentiated into a stout basal portion and slender branches. The former is attached to the substratum

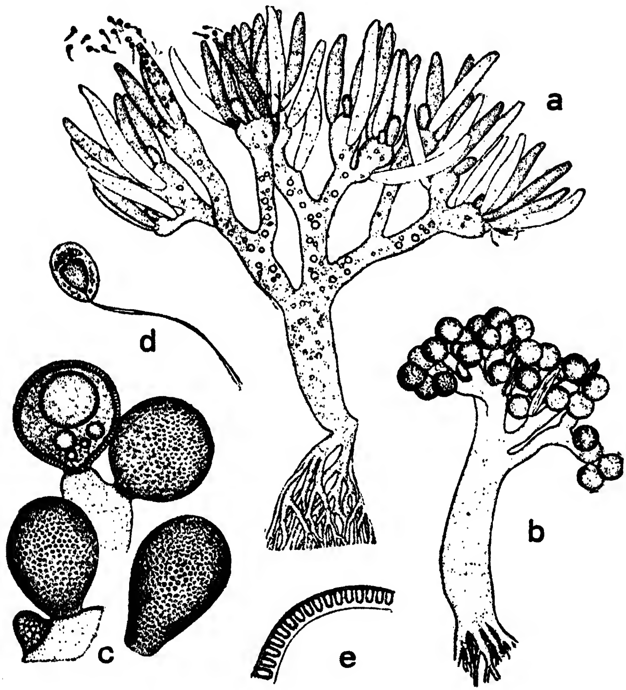

FIG. 51.—*Blastocladia pringsheimii* Reinsch. (*a*) Single large plant showing portion of rhizoid system; branches bearing sporangia and young resting spores. (*b*) Smaller plant bearing spherical resting spores. (*c*) Resting spores. (*d*) Swarmspore. (*e*) Optical section of wall of resting spore. (*After Thaxter 1896.*)

by rhizoids. The branches are separated into definite segments by pseudosepta, and are sometimes constricted at the septa (Fig. 50). The pseudosepta, at least in early stages, are perforated, so that the protoplasm of adjacent segments is continuous. The branching of the thallus is dichotomous to sympodial. The sporangium is provided with a varying number

of exit papillae. The members of the genus seem to prefer animal substrata, being found on dead flies, bones, etc., in the water.

Four species have been described which belong beyond question in this genus. They are *Allomyces arbuscula* Butler (1911: 1023), *Blastocladia strangulata* Barrett (1912: 353), *Septocladia dichotoma* Coker & Grant (1922: 180), and *Allomyces javanicus* Kniep (1929). The first three are perhaps identical, but the various workers who have published on the group do not agree in their treatments. The student should consult von Minden (1916: 214), Fitzpatrick (1923: 166), and Kanouse (1927: 303), as well as the original papers.

3. **Blastocladia** Reinsch (1878: 298).

The thallus resembles that of *Allomyces*, but lacks pseudosepta and is not definitely constricted (Fig. 51). The sporangium is provided with only a single exit papilla. The genus includes at present seven species. All were found growing saprophytically on submerged plant substrata. The most complete treatment of the genus is that of Kanouse (1927: 297) but the papers of Thaxter (1896: 45) and von Minden (1916: 189) also should be consulted.

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CHAPTER VI

MONOBLEPHARIDALES

The members of this order differ strikingly from the Saprolegniales in that the antheridium frees ciliate male cells (**antherozoids, spermatozoids, sperms**) which swim to the oogonium and fertilize the oosphere. Since this type of fertilization occurs nowhere else in the fungi the group is of unusual interest to the student of phylogeny. That school of mycologists which regards the fungi as a heterogeneous group of degenerate forms, derived at various points from different types of the algal series, finds in this order a convenient intermediate type connecting the Saprolegniales with such algae as *Vaucheria* and *Oedogonium* in which fertilization by spermatozoids occurs. Those students who prefer to derive the higher Phycomycetes from the lower see in the isogamic fusion of zoospore-like cells in certain chytrids the primitive type of sexuality from which the heterogamic copulation existing in the Monoblepharidales has arisen. This second point of view receives support from the recent work of Kniep on *Allomyces javanicus* (p. 132) and from the fact that the oosphere of *Monoblepharis* is characterized to a limited degree by motility.

The existence of this remarkable and interesting group of aquatic fungi was first noted by Cornu (1871: 58). He (1872: 82) founded the genus *Monoblepharis* describing and figuring two species, *M. sphaerica* and *M. polymorpha*, and enumerating a third, *M. prolifera*. The last named species was independently described and figured by Reinsch (1876: 293) under the name, *Saprolegnia siliquaeformis*, only the sporangial stage being seen. Cornu (1877: 227) regarded the species as identical with his *M. prolifera*, and stated that since the publication of his earlier paper he had observed its oospores. He says that these are borne in oogonia resembling the zoosporangia, and result from fertilization of an oosphere by motile spermatozoids. On the basis of this statement and because of the uniciliate character of the zoospores the species has been retained in the group by

various authorities. Fischer (1892: 378) made it the basis of a new genus, *Gonapodya,* and this genus and *Monoblepharis* make up the Monoblepharidineae of his classification and that of Schröter (1893: 106). The statement by Cornu that spermatozoids occur in *M. prolifera* has never been verified by any other worker, and Thaxter (1895: 478) suggests that Cornu may have been misled as to their presence by the great variation in size exhibited by the zoospores in some instances. He feels, moreover, that Cornu's "oospores" may have been merely encysted sporangia. The mycelium of *Gonapodya* differs very strikingly from that of *Monoblepharis*, in being constricted as in the Leptomitaceae, and in most of the recent classifications (Thaxter, 1895: 478; v. Minden, 1912: 576) the genus is included in that family. Here it is incorporated instead in the Blastocladiaceae (p. 134) on account of its uniciliate zoospores and non-cellulose cell walls. Laibach (1927), has recently studied both *Monoblepharis* and *Gonapodya* in stained preparations and, impressed by the similarity of nuclei and cytoplasmic vacuolation in the two genera, advocates the incorporation of *Gonapodya* in the Monoblepharidales on cytological bases.

Following the establishment of the genus *Monoblepharis* by Cornu a period of twenty-five years elapsed before any member of the genus was seen again, some workers coming to doubt the very existence of a genus having the unique characters which he figured and described. However, in 1895, Thaxter described two new species from America, his account corroborating the essentials of Cornu's description. Subsequently, other species have been observed by Thaxter (1903) in America, and by Lagerheim (1900), Woronin (1904), von Minden (1911), and Laibach (1926; 1927) in Europe.

The order is the smallest in the fungi, and as here treated consists of the family Monoblepharidaceae containing the single genus, *Monoblepharis.*

The mycelium of *Monoblepharis* is saprophytic, occurring usually in decaying twigs lying in the water. It is coenocytic and characteristic in aspect. The cytoplasm forms a network of meshes which are regular in size and form, a strikingly uniform vacuolation resulting. The strands of protoplasm tend to cross the hyphae at right angles rather than to run longitudinally as in the Saprolegniales. The fertile hyphae arise from a branching vegetative mycelium which is fixed to the substratum by rhizoids.

They are rigid in habit, usually unbranched, and lack septa other than those cutting off the sexual organs and sporangia.

Except in the species, *M. macrandra* Lag., the oogonia and antheridia are borne together on the same hypha. In fact in certain species the antheridium is borne on the oogonium. It differs from the oogonium in size and shape. The oogonium is a rounded to more or less elongate cell tapering above to a definite beak. Before fertilization it ruptures at the apex, an open mouth resulting through which a portion of the contents is expelled by the violence of the discharge. The remainder of its protoplasm then contracts to form a definite oosphere. The spermatozoids escape from the antheridium through a terminal opening and are uniciliate. They swim about, come to rest on the unfertilized oogonium, crawl over its wall with an amoeboid movement, and find their way into its mouth. A single spermatozoid effects fertilization, sinking slowly into the substance of the oosphere. In some of the species the fertilized oosphere pushes through the mouth of the oogonium and rounds up outside before assuming the thick wall which marks its transformation into the oospore. In other species it matures within the oogonium. Germination of the oospore occurs apparently in all cases by a germ tube.

Accounts presented by different workers on the group are not in agreement with respect to the character of the swarmsporangia and swarmspores. In some of the species large clavate organs resembling the sporangia of *Saprolegnia* occur. In these are formed uniciliate cells, which Lagerheim regards as swarmspores. Thaxter's studies indicated that these clavate cells are merely abnormally large antheridia, and he states that intermediate sizes exist between them and the normal smaller type. He says that the sporangia correspond in size and form with the oogonia, and form biciliate swarmspores. Following the appearance of Thaxter's paper Lagerheim founded the genus *Diblepharis* to include the species in which Thaxter had reported biciliate swarmspores, and retained in *Monoblepharis* the species in which he believed the swarmspores to be uniciliate. Later Thaxter (1903) reported the biciliate condition in one of Lagerheim's own species. Apparently other workers have never observed biciliate swarmspores, and recently Laibach 1927) suggests that the biciliate cells observed by Thaxter were the swarmspores of some parasite which had attacked the

oosphere. He maintains the position that the swarmspores in all the species are uniciliate. In any case, there seems to be no basis at present for retaining the genus *Diblepharis*.

The genus, *Myrioblepharis*, founded by Thaxter (1895) on a single very remarkable species, *Myr. paradoxa* (Fig. 52), was incorporated in the Monoblepharidales by Lotsy. However, as it is known only in the sporangial stage its position is uncertain. The sporangium is developed terminally and at maturity emits its entire contents as a naked protoplast through an apical opening. This adheres at the mouth as a spherical mass where it rotates rapidly. Proliferation of the sporangium occurs and a second mass is soon pushed out below the first. Proliferation continues rapidly, and as the third mass appears the first breaks up into four, rarely more, multiciliate spores which swim away. This process is repeated many times, a series of twelve or more empty sporangia being sometimes found below the rotating spheres at the tip of the sporangiophore. Since multiciliate zoospores occur in no other genus of fungi the form is of peculiar interest, but there seems to be no reason for including it even as a doubtful species in the present order. The zoospores recall those of the alga, *Vaucheria*. The fungus is discussed by von Minden (1912: 476) on the basis of material collected by him in Germany. He is inclined to regard the multiciliate spores as those of a protozoan parasitic in a species of *Pythium*.

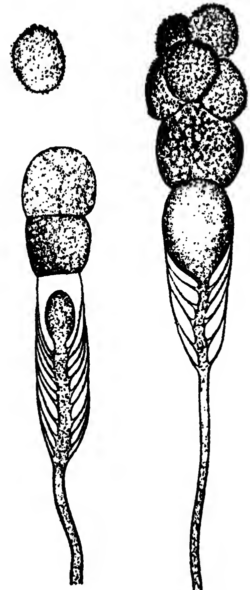

FIG. 52.—*Myrioblepharis paradoxa* Thaxter (*After Thaxter.*)

As here recognized the genus *Monoblepharis* includes six species. They have been separated on rather outstanding characters as follows.

Key to Species of Monoblepharis

I. Oospore normally maturing within the oogonium.
  A. Oospore smooth, antheridium borne on the oogonium.
    1. Oogonia large, normally superposed in single series.
      1. *M. insignis* Thaxter (Fig. 54, *a–d*)
    2. Oogonia small, fasciculate at the tips of the hyphae.
      2. *M. fasciculata* Thaxter (Fig. 54, *e–g*)
  B. Oospore warted, antheridium borne below the oogonium.
      3. *M. sphaerica* Cornu (Fig. 53, *a–c*)

II. Oospore normally maturing outside of the oogonium.
  A. Oospore adherent to the mouth of the oogonium, the antheridium normally borne on the oogonium.
    1. The antheridium borne above the middle third of the oogonium, lacking an abruptly distinguished point of insertion, narrowly cylindrical.
      4. *M. polymorpha* Cornu (Fig. 53, *d–f*)
    2. The antheridium borne below the terminal third of the oogonium, arising from an abruptly distinguished point of insertion, broadly cylindrical.
      5. *M. brachyandra* Lagerheim (Fig. 53, *g–h*)
  B. Oospore falling away from the mouth of the oogonium; oogonia and antheridia normally borne on separate hyphae.
      6. *M. macrandra* (Lag.) Woronin.

Two additional species, known only in the sporangial stage, *M. regignens* Lag. and *M. ovigera* Lag., are omitted because of imperfect knowledge. Laibach (1927) has erected for these the genus *Monoblepharopsis*, and regards it as intermediate between *Monoblepharis* and *Gonapodya*. He recognizes *M. regignens* (Lag.) Laibach without reserve, but suggests the probability that *M. ovigera* (Lag.) Laibach constitutes merely a variation of it. Moreover, Laibach states that *Monoblepharis brachyandra* Lag. represents merely a developmental phase of *M. polymorpha*, and intimates that *M. insignis* Thaxter and *M. fasciculata* Thaxter belong in the same category.

Although Lagerheim presented isolated facts concerning the cytology of *Monoblepharis* our knowledge of the nuclear history in the genus rests almost wholly on the recent researches of Laibach. Both writers state that the oogonium is uninucleate in the beginning and remains so until after fertilization. In this respect the female organ differs strikingly from that of any other known member of the Oomycetes. Here the term gamete, rather than coenogamete, may be correctly applied (p. 31).

According to Laibach's account the sporangium and antheridium are both multinucleate in the beginning, and differ only in the number and size of the ciliate cells which are formed, the spermatozoids being fewer and smaller.

After the male nucleus enters the oosphere the sex nuclei may rest side by side for a considerable period before fusion takes

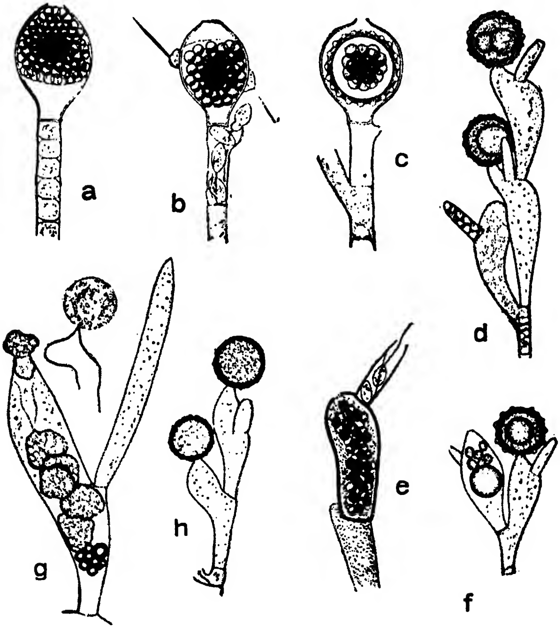

FIG 53.—(*a–c*) *Monoblepharis sphaerica* Cornu. (*d–f*) *M. polymorpha* Cornu (*g–h*) *M. brachyandra Lag.* (*a,b*) Antheridium below oogonium. (*c*) Mature oospore. (*d–f*) Oogonia and antheridia. (*g*) Swarmsporangium and biciliate swarmspores. (*h*) Mature oospores. (*a, b, c, e, after Cornu; others after Thaxter 1903.*)

place. Reduction of chromosomes apparently occurs in the first division of the fusion nucleus. Several subsequent mitoses occur, and when the germ tube is put out by the oospore as many as sixteen nuclei may be present.

The mycelium is wholly non-septate up to the time of the formation of reproductive cells. Laibach finds that sporangia

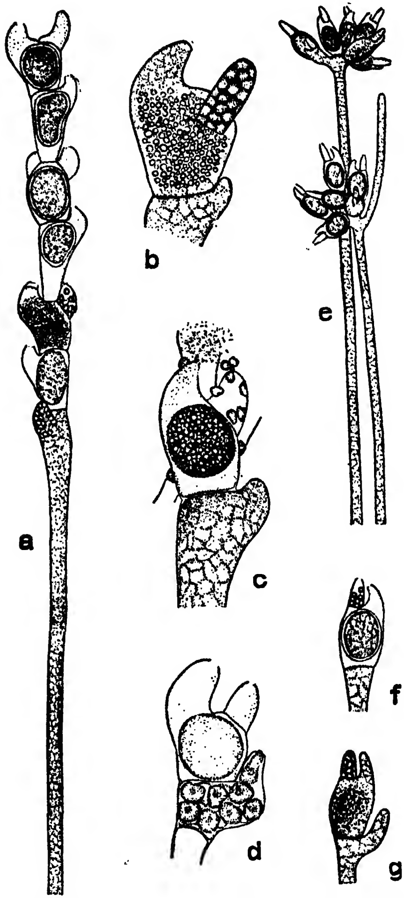

FIG. 54.—(*a–d*) *Monoblepharis insignis* Thaxter. (*e–g*) *M. fasciculata* Thaxter. (*a*) Oogonia in linear series each bearing an antheridium. (*b*) Differentiation of ooplasm and antherozoids. (*c*) Oosphere formed; finely granular periplasm escaping through pore in oogonial wall; uniciliate antherozoids creeping over wall toward pore. (*d*) Fertilized oosphere and swarmsporangium. (*e*) Fasciculate oogonia. (*f*, *g*) Oogonia, oospore, antheridia. Magnification of (*a*) and (*e*) the same; that of others uniform but higher. (*After Thaxter 1895.*)

develop in greatest numbers in fresh water at about 10°C. while antheridia and oogonia appear at higher temperatures especially in polluted water. Oospores may develop in the spring and germinate in the autumn, or develop in the autumn and hibernate until spring.

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CHAPTER VII

SAPROLEGNIALES

The fungi composing this order are commonly termed the water moulds. By certain early students (Pringsheim, 1858: 284) they were incorporated in the algae. They occur more or less abundantly in all fresh waters, usually preferring those which are clear and relatively pure. In stagnant or polluted waters their development is retarded by the presence of bacteria and infusoria. A striking exception exists in the case of *Leptomitus lacteus* which grows in waters containing large amounts of organic substances, such as occur in the drains from certain types of manufacturing establishments, paper mills, sugar factories, etc. The members of the order are usually saprophytic, being often found on plant or animal remains lying in the water. In recent years many species have been isolated from the soil. A few are known to be parasitic. The saprophytic forms occur on a wide variety of substrata including decaying algae, woody or herbaceous parts of vascular plants, the bodies of insects, and other types of non-living organic matter. Practically all the species may be grown in pure culture. Sterilized flies immersed in sterilized water in watch glasses afford perhaps the most commonly used source of nutriment. Bits of egg albumen, ant pupae, aphids, and cooked peas also have been extensively used. More satisfactory and constant results may be obtained if sterilized synthetic media are used, and if isolations are made from single spores or hyphal tips. Marked variation in the development of the mycelium and reproductive bodies may be obtained by altering the chemical constitution of the medium. The physiological treatises of Klebs (1899), Kauffman (1908), Obel (1910), and Pieters (1915 *a*) are extremely important in this connection, and should be consulted before any attempt to do critical taxonomic work is made.

The mycelium of the Saprolegniales is profusely developed. It usually consists of two sorts of hyphae, internal threads (rhizoids) which ramify throughout the substratum and taper

abruptly to pointed ends, and external filaments which arise from the former, float in the water, and have in mass a whitish cottony aspect. The hyphal walls give the test for true cellulose.

Asexual spores are borne in specialized sporangia, and sexual reproduction when present takes place by the formation of antheridia and oogonia which differ from each other strikingly in size and shape. The oogonium is usually more or less globose, and at maturity contains one or more naked protoplasmic oospheres. Later these assume a cellulose wall and are then termed oospores. The antheridium is clavate and smaller than the oogonium. In fertilization a tube put out by the antheridium enters the oogonium and discharges its contents directly into the oosphere. Some species mature their oospores without fertilization and are termed **parthenogenetic or apogamous.** Some lack antheridia entirely and are termed **apandrous.** Ciliate sexual cells are wholly absent. Swarmspores are commonly formed and are always biciliate.

In the development of abundant mycelium and in the formation of morphologically distinct oogonia and antheridia the group shows a marked advance from the condition in the Chytridiales and Ancylistales. In the absence of ciliate sexual cells it is sharply separated from the Monoblepharidales and Blastocladiales. It is clearly most closely related to the Peronosporales, these two orders indeed being so closely connected by intermediate forms that no single absolute point of distinction between them exists as the basis of a taxonomic separation. The Saprolegniales are distinguished in general by their aquatic habit and persistent sporangia, while the Peronosporales for the most part are characterized by a terrestrial habit and deciduous sporangia, the latter often being termed conidia. The members of the family Pythiaceae of the latter order possess characters more or less intermediate between those of the Saprolegniales and Peronosporales, and in some classifications are included in the Saprolegniales.

The order Saprolegniales, as here constituted, contains two families, Saprolegniaceae and Leptomitaceae, embracing a total of nearly one hundred species in about twenty genera.

Key to Families of Saprolegniales

I. Thallus composed of cylindrical branching hyphae lacking definite constrictions.

1. Saprolegniaceae, p. 148

II. Thallus in some forms consisting of cylindrical branching hyphae definitely constricted at intervals; in others differentiated into a prominent stout main axis from which usually arise relatively more slender branches, with or without definite constrictions.
2. **Leptomitaceae,** p. 171

Saprolegniaceae

The hyphae composing the floating external mycelium in this family are of greatest diameter near the point of attachment to the substratum, and decrease slowly toward their outer ends. They are, however, nearly cylindrical. Their branching is usually of the monopodial type, though rarely dichotomous. Septa, other than those cutting off the reproductive cells, are absent; the lumen of the filament consisting of a single continuous branching cavity containing many nuclei. The mycelium is, therefore, coenocytic, as in the majority of the lower Phycomycetes. The hyphal walls are unlike those of higher fungi in that they give the chemical reaction for pure cellulose (*i.e.*, turn blue with chloriodide of zinc). Different species differ greatly in the diameter of their hyphae, the entire range extending approximately from five to one hundred microns. The length of the filaments is determined to an extent by the amount of available nutriment. In soil inhabiting species the mycelium is relatively depauperate, and in culture forms a dense mat of limited extent.

The asexual spores are borne in cylindrical, clavate to globose sporangia which are usually terminal, being cut off by transverse septa at the tips of the hyphal branches. Intercalary sporangia sometimes occur. In *Dictyuchus* they may be cut off terminally in basipetal succession.

The protoplasm of the sporangium is much denser than that in the remainder of the hypha, and is filled with numerous nuclei which flow in from the thread before the septum is formed. Cleavage planes appear in the protoplasm, and by their branching and intersecting the content of the sporangium is split up into a number of small irregularly polyhedral masses each containing a single nucleus. These are the spore origins, each of which finally functions as an independent spore. The phenomena associated with the escape of these spores from the sporangium and their germination differ in different species of the group, and to a considerable extent afford bases for separation of genera.

In several genera the sporangiospores encyst within the sporangium, each spore enveloping itself in a thin cellulose membrane. In other cases the spore is provided with a pair of cilia, and escapes from the sporangium as a zoospore without having first encysted.

In the genus *Aplanes* the sporangiospores may encyst within the sporangium, and then germinate *in situ* by germ tubes which penetrate the sporangial wall and reach the outside. In *Geolegnia* the encysted sporangiospores are thick-walled and remain quiescent in the sporangium until freed by the disintegration of its wall. They then germinate by germ tubes, zoospores being unknown. In *Thraustotheca*, *Calyptralegnia*, *Dictyuchus*, and *Brevilegnia* the spore after encysting within the sporangium germinates, usually by the emission of a biciliate zoospore which swims about and finally encysts again before germinating by a tube. In *Thraustotheca*, *Calyptralegnia*, and *Brevilegnia* the encysted spores escape from the sporangium before germinating. In *Dictyuchus* the zoospores on escaping from the cysts pass to the outside through individual pores in the sporangial wall. In *Thraustotheca*, *Calyptralegnia*, and *Brevilegnia* the wall either disintegrates or is ruptured by the expansion of the swelling spores within; the spores escaping in a more or less indefinite manner through an opening of indeterminate size. In all the remaining genera of the family the spores, instead of encysting within the sporangium, escape as biciliate zoospores through a small pore at its tip. In *Achlya* and *Aphanomyces* the escaping spores reach the water just outside the mouth of the sporangium, and there become encysted, each spore rounding up and assuming a delicate membrane. The escaping spores thus form a more or less spherical aggregation at the mouth of the sporangium. Their failure to separate from one another on reaching the water has been explained by Hartog as due to a mutual attraction, perhaps chemical in nature, to which he applies the term **adelphotaxy** (Couch, 1924 *a*; Lounsbury, 1927). After a period of rest at the mouth of the sporangium each spore slips from its membrane, these being left behind as empty spheres. The escaping zoospores are reniform (bean-shaped) and biciliate, the cilia arising together at the lateral depression corresponding to the hilum of the bean. After a period of swarming in which the zoospores swim about actively they come to rest and encyst again, the encysted spores being termed **cystospores**. They finally ger-

minate by a germ tube which develops directly into mycelium. In *Saprolegnia*, *Isoachlya*, and *Leptolegnia* the zoospores escape separately into the water and swim away instead of encysting at the mouth of the sporangium. They are ovoid or pit-shaped, and swim by means of two cilia attached at the forward more pointed end. After a period of motility they encyst separately and, later, escaping from the membrane, swarm again. In the second period of motility they are reniform with two lateral cilia. At the close of the second swarming period they encyst and germinate by germ tube. In *Protoachlya* some of the spores escape immediately as in *Saprolegnia* while the remainder encyst at the mouth of the sporangium as in *Achlya*. In these genera the zoospores are termed **diplanetic** on account of the two periods of swarming, the phenomenon of **diplanetism** exhibited here contrasting with **monoplanetism** in those genera in which only a single swarming occurs, and with **aplanetism** in *Aplanes* and *Geolegnia*. The spores of *Achlya* and *Aphanomyces* are regarded as diplanetic but the first swarming period is very brief, being confined to the sporangium, and serves only to carry the spores through the terminal pore. In *Achlya* the spores during this period correspond to those of the first type in *Saprolegnia*, and this is probably also the case in *Aphanomyces*, although the narrow diameter of the sporangium in this genus makes demonstration of the fact difficult. In *Thraustotheca* the spores are of the second type and definitely monoplanetic. In *Pythiopsis* they are monoplanetic, but strangely enough are of the first type. The spores of *Dictyuchus* have been regarded as monoplanetic, but in recent years a peculiar condition has been shown (Weston 1919) to exist in this genus. The spores which escape from the sporangium are of the reniform type. After swarming they encyst and later under favorable conditions may swarm again, though germination by a tube often occurs. The spores in the second swarming period are reniform and laterally biciliate as in the first period. Following the second swarming, encystment and germ tube formation occur. This condition of **"repeated zoospore emergence"** in *Dictyuchus* is perhaps present also in other genera, having been merely overlooked. It seems to be present in *Pythiopsis intermedia* where the zoospore is of the first type. The two swarming periods in such cases are not to be confused with true diplanetism in which zoospores of two distinct types follow each other always in the same order. The

condition in *Dictyuchus* is properly to be regarded merely as a variation in the process of germination.

The existence in the Saprolegniaceae of zoospores of two different forms has not been satisfactorily explained. Some authors have suggested that the reniform spore is the primitive type and the ovoid spore a more recent development. In this connection it is of interest to note that the zoospores of the Peronosporales are always of the reniform type. Atkinson (1909) gives, as evidence of the monophyletic nature of the fungi, data indicating that the phenomenon of diplanetism as present in the Saprolegniaceae has gradually evolved through the Chytridiales and Ancylistales.

The first sporangium formed from a hypha may be called the primary sporangium. After the escape of the zoospores a second sporangium may be developed, then a third, and so on until several are present. The secondary sporangium and those which follow it arise by one of several different methods. In *Saprolegnia* and *Leptolegnia* the new sporangium is initiated by the upward growth of the septum at the base of the old one, and soon fills the old cavity more or less completely. The hypha may even grow through the mouth of the old sporangium, and cut off the new sporangium at a considerable distance beyond its tip. Several new sporangia may be developed in turn within the wall of the primary sporangium. This phenomenon has been termed **proliferation.** In *Achlya, Aphanomyces, Pythiopsis,* and *Thraustotheca* cymose branching of the hypha occurs in the development of new sporangia, lateral sporangia growing out below the primary, and proliferation being absent. In *Isoachlya* and *Protoachlya* cymose branching and proliferation may both occur together. Sometimes sporangia are cut off in basipetal succession (*Dictyuchus*). Rarely intercalary sporangia occur.

Certain sporangia, after being cut off from the hyphae, may remain quiescent for a considerable period, and later discharge their spores in the usual manner. In such cases the term **resting sporangium** has been applied. These are merely ordinary sporangia whose development has been temporarily arrested, perhaps by conditions of the environment. They are sometimes shorter and broader than the typical sporangia.

The term **chlamydospore** has been given to another type of non-sexual reproductive body formed in many species of the

family. These bodies are usually developed at the ends of the hyphae in chains. They are unicellular, globose to ovoid or pyriform, thick-walled resting spores, and fall apart easily at the dividing septa. After a resting period of variable length they germinate by a germ tube on which a sporangium is usually soon formed. The chlamydospore never germinates directly by swarmspores, and in this respect differs distinctly from the resting sporangium. Chlamydospores are often developed abundantly, and species occur (Humphrey, 1893: 83; Weston, 1917) in which the sexual spores seem to have been completely replaced by them. Some authors avoid the term chlamydospore, preferring **gemma, conidium,** or **resting spore.**

The sexual organs are developed on the external mycelium, and are usually terminal in position, though occasionally intercalary. The oogonium, arises as a swelling of the hypha which bears it (oogonial branch), and at maturity is definite in form. If terminal it is usually more or less globose, if intercalary barrel-shaped. Its wall becomes thickened by the deposit of new material on the inner surface, this new layer failing to give the reaction for true cellulose characteristic of the primary wall. Scattered over the wall in some species a varying number of small circular thin spots or pits occur. These constitute points at which the secondary thickening has failed to take place. It was formerly supposed that the fertilization tubes from the antheridia enter at these spots, but this has been shown not to be necessarily true. Though the function of the pits is unknown they are striking in appearance and of taxonomic importance in certain forms.

The antheridial branches are slender and lateral. The antheridium is cut off at the tip of the antheridial branch. It is cylindrical or clavate in form, and somewhat thicker than the branch. It is usually applied to the oogonium in such a fashion that its side rather than its tip is in contact with the oogonial wall. In some species antheridia are absent or only rarely formed. Not infrequently several are found attached to a single oogonium.

The same primary hypha may bear both oogonial and antheridial branches or only those of one sex. In ordinary cultures it is often impossible to determine whether two hyphae belong to the same or different thalli, and since single spores have been used as the starting point for cultures in only a few cases, it

has not been possible for workers to apply with certainty the terms **monoecious** or **dioecious,** or more correctly the terms **homothallic** and **heterothallic.** De Bary's terms diclinous and androgynous have been commonly used. When a single hypha gives rise to both oogonial and antheridial filaments the species is termed **androgynous.** In such cases antheridia may attach themselves to oogonia from the same or other filaments. If a single main hypha bears filaments of only one sex and those of the other sex come from a distance and seem to arise from other hyphae the species is **diclinous.** Androgynous species have been assumed to be homothallic and diclinous species heterothallic. True heterothallism has been demonstrated by Couch (1924 *b*) in *Dictyuchus monosporus* and *Achlya bisexualis* (Coker, 1927: 208), and will doubtless be found in other forms.

The protoplasmic content of the oogonium is at first homogeneous, but it soon becomes differentiated into denser more or less isodiametric portions separated by intervening avenues of clear cell sap. These naked protoplasmic bodies gradually contract and become spherical in form. They are then termed **oospheres.** The reserve food supply present in the oosphere exists in the form of globules of fatty material. The aspect of the oosphere when fully formed is one of two types depending upon the position and size of these globules. In all cases the fatty reserve lies near the periphery, but in one type it is in the form of small droplets entirely surrounding the protoplasm, while in the other it is collected into one or a few large drops on one side. In the latter type the oosphere has a lopsided aspect and is termed **eccentric.** In the former it is called **centric,** while intermediate types may be termed **subcentric.** Coker regards this situation as of considerable systematic significance, and says that one type of oosphere is constant in a given species and often throughout a genus. Finally each oosphere secretes a cellulose wall about itself, and is then called an **oospore.** The oospore at maturity is smooth in all known cases.

As soon as the oospheres are differentiated the antheridia form delicate **fertilization tubes** which penetrate the wall of the oogonium and branch in its interior, the tip of each branch finally reaching an oosphere and coming into actual contact with it. Earlier writers assumed from the fact of the presence of the fertilization tubes and from analogy with other fungi that actual

fertilization occurs. De Bary, failing to note the discharge of the content of the tube into the oosphere, was the first to question it. He studied living material of several species of *Saprolegnia*, and concluded that even in those cases in which the fertilization tubes reach the oospheres they fail to rupture and fertilize them. Parthenógenesis was believed by him to be usual in the group, and his views have subsequently been maintained by various students including Marshall Ward, Hartog, and Davis. The early work on the problem was done on living material. Consequently the study of nuclear phenomena was impossible, and the actual fusion of sex nuclei could not be demonstrated. Later, with the advent of modern cytological technique, various workers have sought to solve the problem of sexuality in the group. Unfortunately the results have been diverse, and a bitter controversy has ensued.

Trow has published several papers in which he claims to have demonstrated a true fertilization and a fusion of sexual nuclei in several species of *Achlya* and *Saprolegnia*. His statements have been severely attacked by Hartog and later by Davis, both of whom are firm in the conviction that parthenogenesis is present throughout the group. Consequently, our knowledge of the sexuality of these forms is in a state of uncertainty. The papers of Hartog (1896; 1899), Trow (1895; 1899; 1904), and Davis (1903) afford interesting reading on account of the frequently caustic criticisms which they contain. The fact that in cytological investigation interpretation plays an important role is well illustrated by the work on this group.

The oogonium of the Saprolegniaceae in the young condition is multinucleate. When the oospheres round up they also are multinucleate, the number of nuclei in the oogonium greatly exceeding the number of oospheres formed. The oospheres at maturity are, however, uninucleate. To explain the disappearance of the remainder of the nuclei two theories have been advanced. Hartog maintains that nuclear fusions many times repeated reduce the number until only one nucleus remains in each oosphere. Trow and Davis believe that the supernumerary nuclei degenerate. Occasionally fully formed oospheres are found to be binucleate. Hartog considers such cases as merely the last stage in the general nuclear fusion. Davis feels that they represent those instances in which two nuclei happen to lie near a coenocentrum, and are thus both saved from degeneration.

Trow believes that they constitute evidence of a true fertilization. He states that one of the nuclei in each binucleate oosphere is a male nucleus introduced by an antheridial tube. He says that while the fully formed naked oosphere is uninucleate, young oospores with very delicate membranes contain two nuclei one of which is often found in the periphery near the fertilization tube, and older oospores with thicker membranes each contain a single large central nucleus.

It is generally known that certain species of the group are apandrous, the antheridia never being formed, and even Trow agrees that in such cases fertilization does not occur. In the light of the fact that degeneration of the typical sexual process appears to be taking place in various groups of the fungi, it seems not illogical to conclude from the data at hand that conditions differ in different species, and to agree with the conclusion of Trow that some species (*S. dioica*) are typically sexual, others (*S. thureti*) obviously apogamous, while between the extremes intermediate conditions exist. In recent years a true fertilization has been described by Claussen (1908) for *Saprolegnia monoica*, by Mücke (1908) for *Achlya polyandra*, by Patterson (1927) for *Achlya colorata*, and by Kasanowsky (1911) for *Aphanomyces laevis*, while in the related groups, Pythiaceae, Leptomitaceae, and Peronosporaceae, the antheridia apparently function in all cases.

In apogamous species the spores developed in the oogonium might well be termed **aboospores** since they correspond to the **azygospores** of the Zygomycetes. The number of oospores in an oogonium is extremely variable in some species while rather constant in others. In certain species of *Saprolegnia* and *Achlya* an oogonium not infrequently contains fifty or more oospores, though the number is usually much less. In the genera *Pythiopsis*, *Dictyuchus*, *Aphanomyces*, *Brevilegnia*, *Geolegnia*, and *Leptolegnia* a single oospore is usually developed, these genera indicating in this respect evolution toward the condition in the higher Oomycetes. After a period of rest germination of the oospore occurs. The inner membrane of the spore is pushed out through a crack in the outer wall and develops into a germ tube. This tube may come into contact with available nutriment, put out rhizoids, and develop directly into a new plant. More often after a brief period of elongation it cuts off at its apex a sporangium typical of the genus, and forms **sporangiospores.**

The single nucleus of the mature oospore undergoes repeated divisions to furnish the nuclei for the sporangiospores, these divisions taking place, in some species at least, before germination occurs.

The most recent monographs on the family are those of Coker (1923) and von Minden (1912), but those of Schröter (1893), Fischer (1892), and Humphrey (1893) will also be found valuable. Since a number of papers have appeared recently containing descriptions of new genera and species no one of the larger monographs is wholly complete. As a result of an investigation of the soil for "water moulds" Coker and his co-workers have described a number of forms which in the light of earlier work are extremely atypical. Several new genera (*Calyptralegnia, Geolegnia, Brevilegnia, Protoachlya,* and *Isoachlya*) have been described. In some cases these are based on forms intermediate in type between members of older established genera. While the writer is unprepared in the light of present knowledge to accept all of these genera as good, it seems best to incorporate them in the key, and give them adequate discussion in order that the student may orient himself clearly regarding the present status of the group.

Key to Genera of Saprolegniaceae

I. Sporangiospores normally encysting within the sporangium.
  A. Oogonium containing more than one oosphere.
    1. Sporangia extremely rare; behavior of sporangiospores very imperfectly known; their germination *in situ* by germ tube occurring at least at times; oogonium provided with an exceptionally thick, prominently pitted wall.
       1. **Aplanes**, p. 158
    2. Sporangia abundant; encysted sporangiospores germinating after their escape from the sporangium; wall of oogonium not of unusual thickness.
      a. Dehiscence of sporangium not occurring at a definite point; the wall either deliquescent throughout, or ruptured by internal pressure so that a wide opening of indeterminate position results; sporangiospores germinating by swarmspores or by germ tubes; oosphere eccentric.
         2. **Thraustotheca**, p. 160
      b. Dehiscence of sporangium accomplished by breaking off of an apical cap, leaving a wide opening through which the swelling spores escape intermittently in

groups prior to their germination by swarmspores; oosphere typically centric with many oil drops.

3. **Calyptralegnia,** p. 162

B. Oogonium containing a single eccentric oosphere.

1. Mycelium well developed, of the usual water mould type, not depauperate; sporangiospores after encysting within the sporangium, escaping from the cysts as laterally biciliate swarmspores and passing to the outside through individual pores in the sporangial wall; the emptied polyhedral cyst walls giving the emptied sporangium the aspect of a net.

4. **Dictyuchus,** p. 162

2. Mycelium depauperate, forming a dense opaque mat.

a. Sporangium in form and method of dehiscence corresponding to *Thraustotheca;* encysted sporangiospores extremely variable in size and shape; germination by swarmspores or by germ tubes in different species.

5. **Brevilegnia,** p. 164

b. Sporangium containing a single row of large spherical to elongate encysted spores which are finally freed by disintegration of the persistent sporangial wall and germinate by germ tube; swarmspores unknown.

6. **Geolegnia,** p. 164

II. Sporangiospores not normally encysting within the sporangium, escaping through a terminal pore.

A. Sporangia typically ovoid, not proliferating; swarmspores monoplanetic, with terminal cilia; oogonia usually 1-spored.

7. **Pythiopsis,** p. 165

B. Sporangia clavate to cylindrical; swarmspores diplanetic.

1. Sporangia usually clavate; swarmspores arranged irregularly in the sporangium; oogonium usually several- to many-spored.

a. Swarmspores escaping separately from the sporangium, not encysting at its mouth.

(1) Sporangia proliferating, the secondary sporangia not developed on lateral branches below the primary.

8. **Saprolegnia,** p. 167

(2) Secondary sporangia arising either by proliferation or by lateral branching.

9. **Isoachlya,** p. 167

b. Some or all of the swarmspores encysting at the mouth of the sporangium.

(1) All of the spores encysting; sporangia not proliferating, the secondary developed as lateral branches below the primary.

10. **Achlya,** p. 167

(2) Some of the spores encysting in an irregular clump, the others swimming away at once; secondary sporangia usually developed as lateral branches below the primary but sometimes formed by proliferation.

11. **Protoachlya**, p. 167

2. Sporangia not clavate; oogonia usually 1-spored.

a. Sporangium of very irregular and complex form; consisting of a much inflated branching basal portion in which swarmspores are formed in several series, and a slender elongate filamentous apical portion in which they are cut out in a single row; the filamentous portion acting as an exit tube through which all the swarmspores pass; swarmspores encysting at the mouth of the tube as in *Aphanomyces*.

12. **Plectospira**, p. 167

b. Sporangium cylindrical, thread-like; swarmspores arranged in a single row in the sporangium.

(1) Swarmspores encysting at the mouth of the sporangium as in *Achlya*.

13. **Aphanomyces**, p. 167

(2) Swarmspores escaping separately as in *Saprolegnia*.

14. **Leptolegnia**, p. 170

1. **Aplanes** de Bary (1888: 650).

This genus, as conceived by de Bary, is characterized by the aplanetic nature of the sporangiospores, which, instead of leaving the sporangium, germinate *in situ* by germ tubes. In other essential respects the genus as described by de Bary resembles *Achlya*. He founded the genus on a single species, *Aplanes androgynus* (Archer) Humphrey (Fig. 55). This species is relatively rare, and, though reported five times from various parts of Europe, is as yet unknown from North America. The genus has long been regarded as doubtful (Weston, 1919: 289), the sporangia being extremely uncommon, and their behavior having been variously described.

In recent years Coker (1923: 76; 1927: 216) has considerably modified the generic concept, and has included two additional species, *A. treleaseanus* (Humphrey) Coker and *A. turfosus* (v. Minden) Coker, representing transfers from *Achlya* and *Saprolegnia*. He feels that observations made on the sporangial stage of these three species have been too few and contradictory to justify conclusions, but regards the sexual stage as distinctive. The wall of the oogonium is said to be thicker than in other

members of the family (reaching four microns), and is prominently pitted. The antheridial branches arise immediately below the oogonium, or if the oogonia occur in chains, as is frequently the case in *A. androgynus*, then the antheridial branch arises near the top of one oogonium and applies itself to the next one above. Since a fourth species, *Saprolegnia hypogyna* Pringsheim, with a similar sexual stage is retained by Coker in

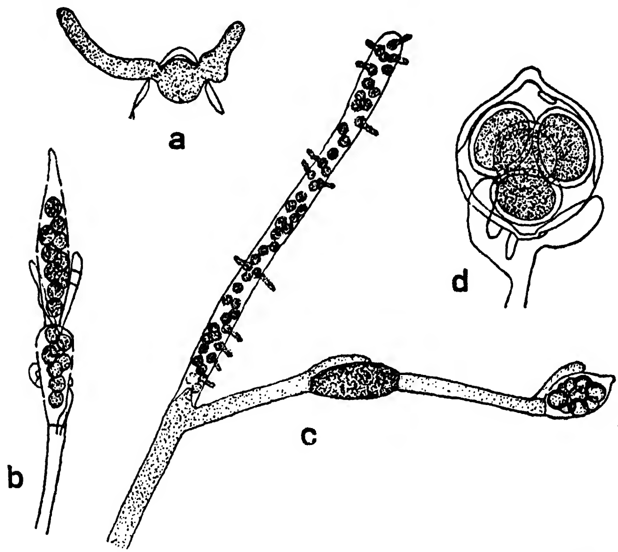

Fig. 55.—(*a–c*) *Aplanes androgynus* (Archer) Humphrey. (*a*) Tip of oogonium showing single germinating oospore. (*b*) Two oogonia with oospores and pitted walls; antheridial branch in each case attached to the cell beneath. (*c*) Sporangium in which sporangiospores are germinating *in situ;* and two oogonia each accompanied by an antheridial branch. (*d*) *Aplanes treleasanus* (Humphrey) Coker. Oogonium, oospores, and antheridial branches. (*a–c, after deBary 1888; d after Coker 1923.*)

Saprolegnia on the basis of sporangial characters the status of the genus *Aplanes* would seem to be doubtful at best. Coker states in the case of *A. treleaseanus*, that though the sporangiospores usually germinate *in situ* by tube, they sometimes emit swarmspores as in *Achlya* or more rarely as in *Dictyuchus*. Further investigation of the sporangial stage of the species incorporated in *Aplanes* is desirable, and may result in the abandonment

of the genus and the inclusion of these species in *Achlya* and *Saprolegnia*. It should be emphasized in this connection that the sporangiospores of various members of the family may germinate *in situ* under certain adverse environmental conditions.

2. **Thraustotheca** Humphrey (1893: 131).

Until recently the type species, *T. clavata* (de Bary) Humphrey, comprised the genus. Although relatively rare it occurs both in Europe and America, and has been studied by various investigators. Earlier workers (Humphrey, 1893: 131) believed the

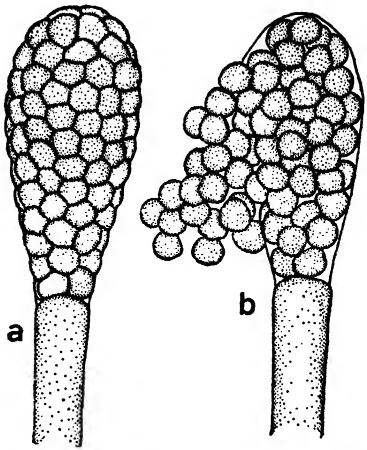

FIG. 56.—*Thraustotheca clavata* (de Bary) Humphrey. (*a*) Mature sporangium. (*b*) Escape of sporangiospores (*After Weston 1918.*)

sporangial wall to be very fragile, and described the encysted sporangiospores as escaping only by its disintegration. This view has been taken also by Coker and Hyman (1912: 88). On the other hand Weston (1918: 160) finds that swelling of the spores, due to imbibition of water, causes an internal pressure which ruptures a normally thick sporangial wall (Fig. 56). The opening which results is usually large and may occur at any point. The spores thus freed then germinate, some by germ tube, others by emission of a reniform, laterally biciliate zoospore (Fig. 57).

The genus at present contains one other species, *T. primoachlya* Coker & Couch (1924: 197). In it the sporangium is said to

function at times as in *Achlya*. A third species referred to the genus as *T. achlyoides* Coker & Couch (1923: 112) has since

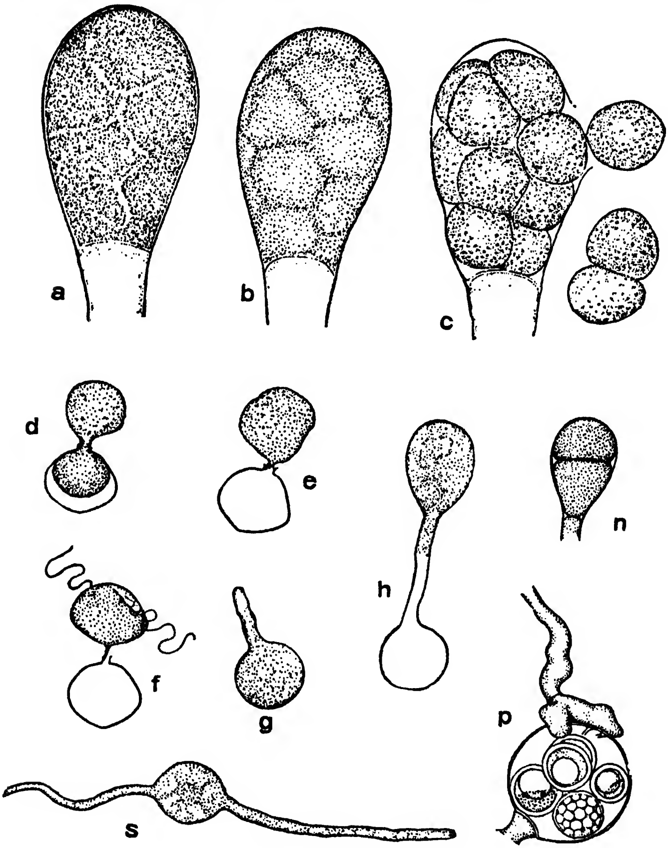

FIG. 57.—*Thraustotheca clavata* (de Bary) Humphrey. (*a–c*) An unusually small sporangium, showing delimitation and escape of sporangiospores. (*d–f*) Liberation of swarmspore from sporangiospore. (*g*, *s*) Germination of cystospore (encysted swarmspore) by germ tube. (*h*) Cystospore forming dwarf sporangium. (*n*) Two-spored dwarf sporangium. (*p*) Oogonium accompanied by antheridial branch. (*After Weston 1918.*)

been made the basis of the genus *Calyptralegnia* Coker (1927: 219); while a fourth species, *T. unisperma* Coker & Braxton

(1926: 140) and a variety *T. unisperma* var. *litoralis* Coker & Braxton (1926: 141) have been transferred to *Brevilegnia* (Coker 1927: 213).

3. **Calyptralegnia** Coker (1927: 219).

This most recently described genus of the family is based on a single species, *C. achlyoides*, which had been described earlier as *Thraustotheca achlyoides* Coker & Couch (1923: 112). The species was isolated from the soil. Though it is not in all respects a typical *Thraustotheca* it would seem to fall very near that genus, and its removal will be questioned by some students.

In *Calyptralegnia*, as the genus is characterized by Coker, the oosphere is typically centric, and in dehiscence of the sporangium an apical cap or segment falls away exposing the spores, which then swell and emerge in successive groups. Since this type of dehiscence has not been previously described, and may prove inconstant, the validity of the genus is in question until the species has been more extensively investigated.

4. **Dictyuchus** Leitgeb (*Bot. Zeitung*, **26**: 502, 1868).

This is a small but extremely interesting genus. Four named species, *D. magnusii* Lindstedt (Humphrey, 1893: 132), *D. sterile* Coker (1923: 151), *D. achlyoides* Coker (1927: 218), and *D. monosporus* Leitgeb (Couch, 1924 *b*: 116) as well as two unnamed species (Fig. 58) studied by Weston (1919: 287) and Coker and Braxton (1926: 144) respectively have been reported from North America. The genus is discussed by Coker (1923), and reference made to a few additional forms known abroad. Except in the doubtful species, *D. polysporus* Lindstedt the oogonia are monosporic. The genus is outstanding from the fact that both heterothallic (Couch, 1924 *b*: 116) and homothallic (Coker and Braxton, 1926: 144) strains have been demonstrated to exist. The work of Couch on heterothallism is being continued and may be expected to result in a better understanding of forms known thus far only in the sporangial condition. In other genera of the family heterothallism is as yet unknown except in a single species of *Achlya* (Coker, 1927: 207).

The genus *Dictyuchus* is characterized chiefly by the behavior of the sporangiospores which after encysting in the sporangium, escape from the cysts through individual pores in the sporangial wall and swim away as reniform laterally biciliate zoospores.

The empty polyhedral cyst walls give the emptied sporangium the aspect of a net; hence the genus name. The sporangia are usually fusiform, new ones being formed in basipetal succession

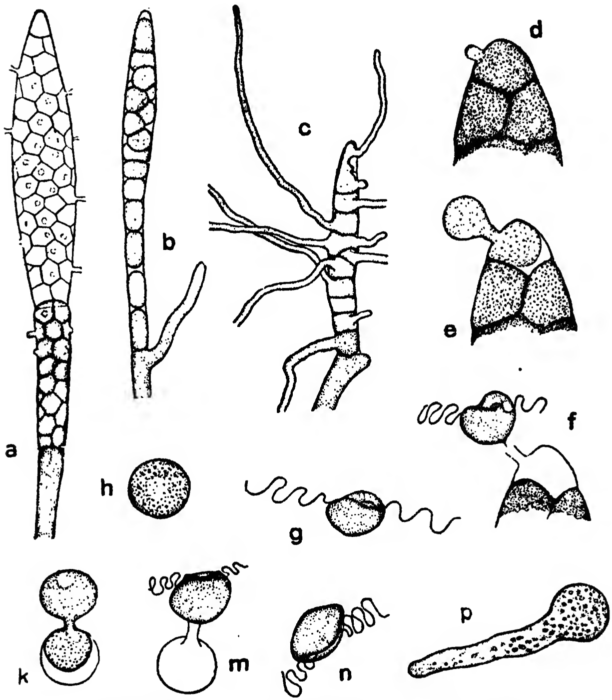

FIG. 58.—*Dictyuchus sp.* (*a*) Two successively formed sporangia, the terminal one empty and showing the "cell net" structure, the second still containing the spores. (*b*) An atypical sporangium developed from a starved hypha, showing incomplete contact of adjacent spores. (*c*) Germination of sporangiospores *in situ*. (*d–p*) A series of drawings illustrating "successive zoospore emergence." (*d, e*) Escape from sporangium. (*f, g*) First motile period; spore reniform and biciliate. (*h*) Encysted zoospore. (*k*) Second emergence. (*m, n*) Second swarming period; same type as first. (*p*) Final encystment and germination. (*After Weston 1919.*)

or by sympodial branching. It is of interest to note that they frequently fall away from each other and from the hypha, and lie free in the water. This deciduous character of the sporangium is unusual in this order, though common in the next. Its

function in this case is not clear. In *D. achlyoides* the sporangia which appear first are said by Coker to free their spores as in *Achlya*, while those which form later are typical of *Dictyuchus*. The achlyoid condition has not been reported in other species.

5. **Brevilegnia** Coker & Couch (Coker, 1927: 207).

In addition to the type species, *B. subclavata* Couch (1927: 229) the genus at present includes *B. unisperma* Coker & Braxton (Coker, 1927: 213), *B. unisperma* var. *litoralis* Coker & Braxton (Coker, 1927: 213), *B. unisperma* var. *montana* Coker (1927: 213), *B. unisperma* var. *delica* Coker (1927: 214), *B. linearis* Coker (1927: 214), *B. bispora* Couch (1927: 228), and *B. diclina* Harvey (1927: 245). All of these have been found only in the soil.

As indicated in the key to genera this genus differs from *Thraustotheca* chiefly in that the oogonium is monosporic. The sporangial stage here is essentially the same as in that genus though the sporangiospores are strikingly variable in size and shape. The mycelium forms a dense opaque mat; the well developed growth typical of water moulds having been lost, presumably as a result of the changed environment. The sporangiospores germinate in some cases by germ tube. In one species, *B. bispora*, the sporangia first formed germinate as in *Achlya*. In view of the variation which exists in the family some students will prefer to widen the limits of *Thraustotheca* to include these forms rather than to recognize this new genus.

6. **Geolegnia** Coker (in Harvey 1925: 153).

The genus contains only the two species on which it was based, *G. inflata* Coker & Harvey and *G. septisporangia* Coker & Harvey (Harvey, 1925: 153; 1928: 552), both isolated from the soil. The mycelium forms a dense opaque mat as in the preceding genus. The sporangial stage is characteristic, zoospores being wholly unknown.

Very large thick-walled sporangiospores lie encysted in a single row giving in early stages an aspect recalling *Leptolegnia*. The sporangium is inflated at intervals or collapsed between contiguous spores in such a manner as to appear almost moniliform at maturity. The spores are freed by disintegration of the sporangial wall, and germinate by tube. The oogonium is monosporic, the oosphere is eccentric, and the antheridia are androgynous.

7. **Pythiopsis** de Bary (1888: 632).

The type species, *P. cymosa* de Bary (Fig. 59), has been studied in North America by Humphrey (1893: 113) and Coker (1923: 18). Two other species, *P. humphreyana* Coker (1914: 292) and *P. intermedia* Coker & Harvey (Harvey 1925: 157) have been added to the genus in recent years. The sporangia of *P. cymosa* are ovoid and recall those of *Pythium*, but in the other species great variation occurs, the sporangium sometimes being elongate as in *Achlya*. The swarmspores as they emerge from the

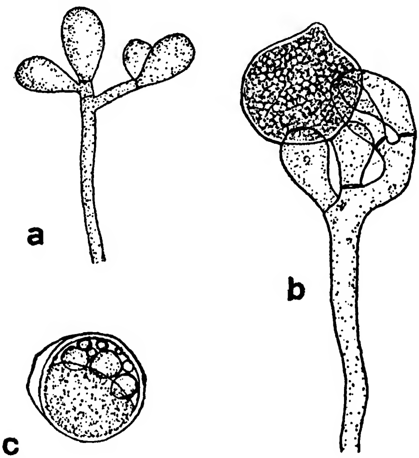

FIG. 59.—*Pythiopsis cymosa* de Bary. (*a*) Cymose development of swarmsporangia. (*b*) Oogonium accompanied by antheridia. (*c*) Mature oospore. (*After de Bary 1888.*)

sporangium in this genus are pyriform and terminally biciliate. While monoplanetic as regards form they apparently have been observed to swim twice in *P. intermedia*, thus recalling the phenomenon of repeated zoospore emergence described in *Dictyuchus* by Weston.

The genus differs from *Pythium* in the form of the swarmspore, which is reniform and laterally biciliate in that genus, in the fact that the oogonia though typically monosporic sometimes contain two or more oospores, in the much broader hyphae, and in the manner of sporangial germination.

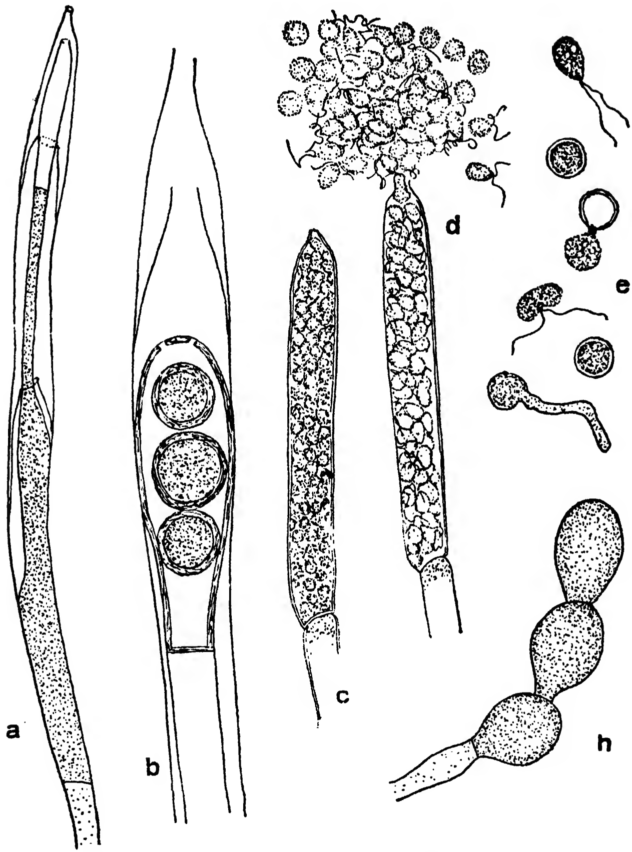

FIG. 60.—*Saprolegnia spp.* (*a*) Proliferation of sporangia. (*b*) An oogonium encased in the walls of two emptied sporangia: a less common phenomenon of proliferation. (*c*) Mature swarmsporangium. (*d*) Swarmspores escaping from a terminal pore. (*e*) Six successive stages (from top to bottom) in diplanetism. (*h*) Chlamydospores. (*a*, *b*, and *h*, *after Coker 1923; c* and *d*, *after Atkinson 1909; e*, *after Marshall Ward 1883.*)

8. **Saprolegnia** Nees von Esenbeck (in Carus 1823: 514).

The genus contains about twenty species some of which are common and widely distributed (Fig. 60). Keys for specific separation are given by Humphrey, Coker, and von Minden. Consult these authors for more detailed information.

9. **Isoachlya** Kauffman (1921: 231).

This genus was recently erected to include several puzzling species whose characters place them on the border line between *Achlya* and *Saprolegnia*. The secondary sporangia arise either by proliferation or by lateral branching, both modes not infrequently being represented on the same main hypha. The swarmspores are definitely diplanetic. As constituted by Kauffman the genus included *I. toruloides* Kauff. & Coker (Fig. 61), *I. paradoxa* (Coker) Kauff. (*Achlya paradoxa* Coker 1914), and *I. monilifera* (de Bary) Kauff. (*Saprolegnia monilifera* de Bary, 1888: 629). Coker (1923: 85) has added two new species, *I. unispora* Coker & Couch and *I. eccentrica* Coker. Moreover, he has removed the species *I. paradoxa*, making it the basis of the new genus *Protoachlya* Coker.

10. **Achlya** Nees von Esenbeck (in Carus 1823: 514).

This is the largest genus of the family, embracing twenty-five or thirty species (Fig. 61). For specific separations consult the keys given by Humphrey, Coker, and von Minden.

11. **Protoachlya** Coker (1923: 90).

This genus is based on a single species, *P. paradoxa* Coker, removed by him from *Isoachlya*.

12. **Plectospira** Drechsler (1927: 294).

This genus includes *P. myriandra* Drechsler and *P. gemmifera* Drechsler (1929), weakly parasitic on tomato and sugar cane rootlets in the greenhouse. The oogonium is terminal or intercalary, and may be accompanied by as many as sixty-five antheridia. The sexual and asexual organs are well figured by the author.

13. **Aphanomyces** de Bary (*Jahrb. Wiss. Bot.*, **2**: 179, 1860).

In the taxonomic treatment by Coker (1923: 160) eight species are described. Of these *A. laevis* de Bary is the best known. The genus corresponds to *Achlya* in the same sense in which *Leptolegnia*

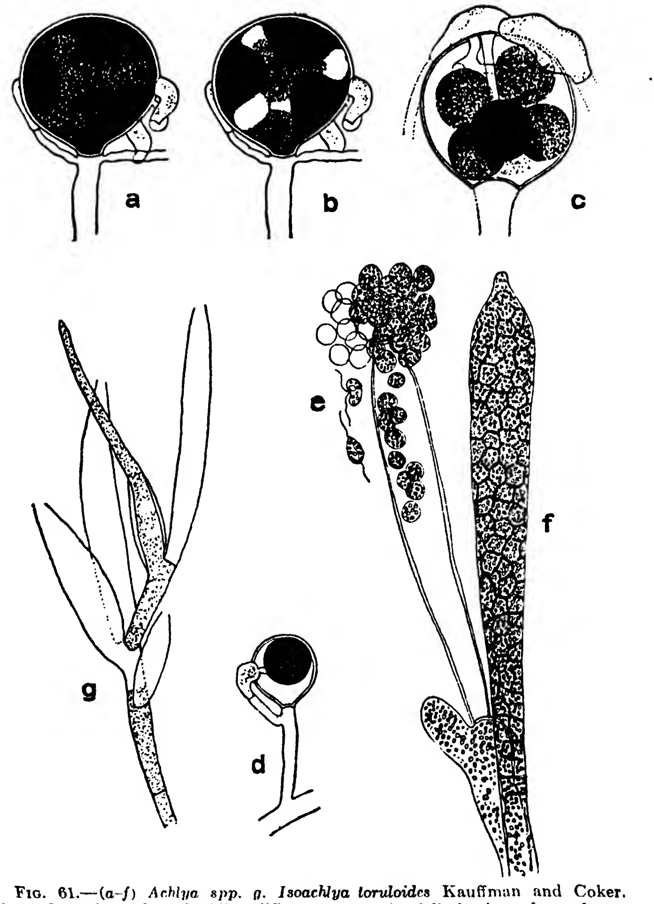

FIG. 61.—(*a–f*) *Achlya spp.* *g.* *Isoachlya toruloides* Kauffman and Coker. (*a–c*) Oogonia and antheridia: different stages in delimitation of oospheres. (*d*) Oogonium with only a single oosphere. (*e*) Sporangium freeing its spores through an apical pore; the spores encysting there and later escaping from the cyst walls as reniform, biciliate, naked swarmspores. (*f*) Mature sporangium with spores already delimited. (*g*) A cluster of empty sporangia which developed in the cymose manner with an accompanying instance of proliferation. (*a–d. after Cornu 1872; e* and *f, after de Bary 1887; g, after Coker 1923.*)

corresponds to *Saprolegnia*. The thread-like sporangium, containing a single row of elongate zoospores, and the one-spored oogonia constitute the chief points of difference (Figs. 62 and 63). A parasitic tendency in the genus is pronounced. Several species are facultative parasites, and *A. phycophilus* de Bary, occurring in *Spirogyra* and *Zygnema* is apparently obligate in its

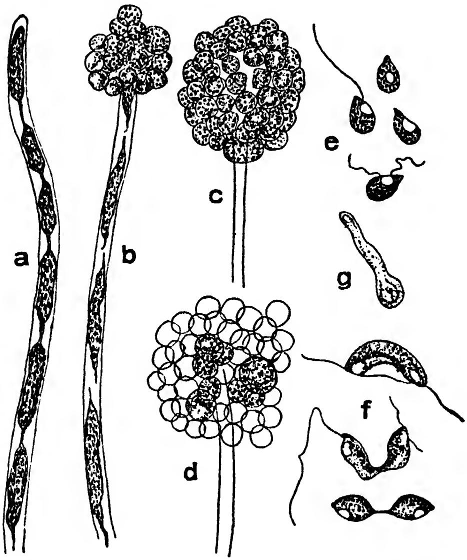

FIG. 62.—*Aphanomyces stellatus* de Bary. (*a*) Portion of mature swarmsporangium showing plasma portions forming swarmspores. (*b*) Plasma portions escaping and collecting as spherical encysted spores at the apex of the sporangium. (*c*) Spherical mass of spores at apex of emptied sporangium. (*d*) Later stage; most of the spores gone leaving emptied cyst walls. (*e*) Mature swarmspores. (*f*) Double swarmspores dividing. (*g*) Germination of spore at close of second encystment to form mycelium. (*After de Bary 1860.*)

parasitism. Many papers have appeared in recent years in reference to the parasitic habit of *A. euteiches* Drechsler which causes a root rot of various plants. This species has been reported on peas (Haenseler, 1926: 467; Jones and Drechsler, 1925: 293), tomatoes (Drechsler, 1927: 287), and other hosts (Linford, 1927: 133). Recently another species, *A. raphani* Kendrick (1927: 19), has been reported as parasitic in roots of

radish. Another, *A. parasiticus* Coker (1923: 165), attacks *Achlya*, and others have been described by Drechsler (1928; 1929) from oats, tomatoes, and beets.

Two somewhat imperfectly known genera, *Aphanomycopsis* Scherffel (1925) and *Sommerstorffia* Arnaudow (1923), fall near *Aphanomyces*. In both of these genera the intramatrical mycelium is characteristically swollen and distorted, and both are based on parasitic species.

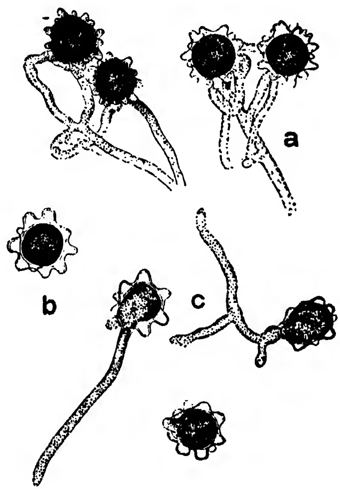

FIG. 63.—*Aphanomyces stellatus* de Bary. (*a*) Hyphae bearing oogonia and antheridia. (*b*) Stellate oogonium with a single spherical oosphere. (*c*) Germinating oospores. (*After de Bary 1860.*)

The genus *Aphanomycopsis* contains the single species, *A. bacillariacearum* Scherffel, occurring in *Pinnularia*, one of the diatoms.

The genus *Sommerstorffia* was based on *S. spinosa* Arnaudow parasitic in the body of Rotiferae. The fungus has been collected in America and has been discussed and figured by Sparrow (1929).

14. **Leptolegnia** de Bary (1888: 631).

Until recently the type species, *L. caudata* de Bary constituted the genus. It has been reported from America only by Coker (1923: 158), but has been studied in Europe by several investi-

gators since de Bary. (v. Minden, 1912: 533.) Two additional species isolated from the soil, *L. subterranea* Coker & Harvey (Harvey, 1925: 158) and *L. eccentrica* Coker (1927: 215) have been recently described.

Doubtful Genus

Jaraia Němec (1913).

This very imperfectly understood genus is known only from the original paper of Němec. It was based by him on a single species, *J. salicis* Němec, isolated from enlargements on living roots of *Salix*, and is regarded by him as an undoubted member of this family. The sporangia and oogonia are extremely irregular in form. The sporangia are provided with several exit tubes. The oogonia are many-spored. Further study will be necessary before the relationships of the form are clearly understood. It is placed in the Blastocladiaceae by Gäumann (1926: 58).

Leptomitaceae

This relatively small family, embracing approximately fifteen species in six genera, includes such a wide diversity of forms that doubt to its phylogenetic unity will probably arise in the mind of the student. The members of the group agree, nevertheless, in several seemingly essential respects. Their membranes are of cellulose, their zoospores are biciliate, and their hyphae are quite definitely and characteristically constricted. As a result of the presence of the constrictions the hyphae have a segmented appearance. Strongly refractive granules of **cellulin**, a carbohydrate material probably allied to cellulose, are present in the protoplasm and provide one of the most characteristic features of the group. These granules are especially prominent near the constrictions, and at times pass into them forming definite plugs with the aspect of thick septa. This occurs particularly in the cutting off of the sporangia and sexual organs. Later the plugs may disappear. True septa are not formed. In the genus *Gonapodya* wholly similar constrictions and cellulin plugs occur, and by some authors the genus is incorporated in this family. A consideration of all the characters of the genus indicates that it is intermediate in type between the Leptomitaceae and Blastocladiaceae, and in the present treatment it is placed in the latter family on account of its non-

cellulose membranes and uniciliate zoospores. As it is known only in the sporangial condition it cannot be assigned to either family with certainty (see p. 130).

In the habit of growth and general morphology of the thallus the family is allied on one side through *Leptomitus* and *Apodachlya* to the Saprolegniaceae, and on the other through *Rhipidium* and *Araiospora* to the Blastocladiaceae. In its sexual stage the group shows relationship with the Pythiaceae. The protoplasm of the oogonium is differentiated into ooplasm and periplasm, fertilization occurs, and a single oospore is formed.

The members of the family are typically aquatic, and occur as saprophytes on vegetable substrata. Few students have concerned themselves with the group, the species being in general infrequently collected though apparently not uncommon. The monographic treatment of the group given by Kanouse (1927) is the most complete.

Key to Genera of Leptomitaceae

I. Thallus not differentiated into a stout trunk and slender branches; composed of cylindrical hyphae which are definitely and characteristically constricted at intervals, and have consequently a segmented appearance.

A. Zoosporangia cylindrical, not differing in form from the hyphal segments; zoospores escaping singly from the sporangium as in *Saprolegnia*.

1. Leptomitus, p. 173

B. Zoosporangia ellipsoidal to pyriform, considerably broader than the segments of the hyphae; zoospores encysting at the mouth of the sporangium as in *Achlya*.

2. Apodachlya, p. 173

II. Thallus differentiated into a stout trunk and slender branches; the latter usually definitely constricted.

A. Trunk more or less definitely cylindrical, corresponding in form to the narrower apical branches.

1. Diameter of trunk not strikingly greater than that of the branches; sporangia of one sort, smooth and broadly clavate; oogonia pyriform; oospore lacking a cellular envelope.

3. Sapromyces, p. 175

2. Diameter of trunk much greater than that of the branches; sporangia of two sorts, one smooth, the other more or less ornamented with spines or finger-like processes; oogonia spherical; oospore surrounded by a cellular envelope.

4. Araiospora, p. 177

B. Trunk not cylindrical.

1. Trunk more or less irregularly lobed or branched, the apical branches slender and bearing the reproductive cells.

5. **Rhipidium,** p. 180

2. Trunk broadly club-shaped and essentially unbranched; reproductive cells borne over its broadened distal end on short pedicels.

6. **Mindeniella,** p. 180

1. **Leptomitus** Agardh (*Systema Algarum,* p. 47, 1824).
syn. *Apodya* Cornu (*Bull. Soc. Bot. France,* **18**: 53, 1871).

This genus contains a single well known species, *L. lacteus* (Roth.) Agardh (Fig. 64), occurring usually in waters strongly polluted by organic material. In favorable locations, such as the drains from sugar factories or breweries, it often forms dense masses of closely felted threads covering surprisingly large areas.

The hyphae are of somewhat smaller diameter at their tips than at their point of attachment to the substratum, but are essentially cylindrical. They are constricted deeply at rather regular intervals, and appear consequently to be composed of definite long segments. Branching occurs usually immediately below the constrictions. Though actually monopodial it may later appear dichotomous.

The most characteristic feature of the species is the transformation in basipetal succession of its hyphal segments to sporangia. The terminal segment frees zoospores through a terminal pore, the constriction at its base being temporarily closed by a cellulin plug. Subterminal segments in turn function as sporangia freeing their zoospores through the constriction into the previously emptied adjacent segment from which they finally reach the outside. Sometimes the subterminal sporangia are provided with lateral exit papillae. Sporangia differing in form from the segments do not occur. Sexual organs are unknown. The zoospores are freed as in *Saprolegnia,* and apparently, as there, are diplanetic

2. **Apodachlya** Pringsheim (1883).

The hyphae resemble those of the preceding genus, but constrictions occur at more frequent intervals. Definite pyriform to broadly ovoid sporangia, considerably broader than the hyphal segments, are borne terminally (Fig. 65). Secondary sporangia are formed by sympodial budding as in *Achlya.* Rarely inter-

calary sporangia occur. The papilla of dehiscence is terminal or lateral. Antheridia are unknown but monosporous oogonia

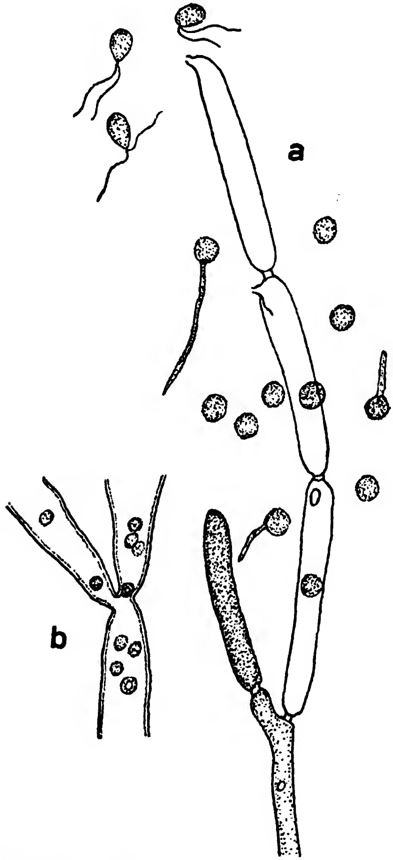

FIG. 64.—*Leptomitus lacteus* (Roth.) Agardh. (*a*) Regularly constricted thread, showing three consecutive segments which have functioned as swarm-sporangia; the swarmspores shown in motile, encysted, and germinating stages. (*b*) Constricted hypha showing swarmspores, cellulin plugs, and absence of septa. (*After Pringsheim 1860.*)

apparently occur. They have not been satisfactorily studied, and are usually referred to as "resting spores." They are

terminal or intercalary, and, in some cases at least, germinate by germ tube. The genus is small, embracing in the treatment of Kanouse (1927: 335) only three species. The inclusion of *A. completa* Humphrey is avoided in that its sporangia have not been seen.

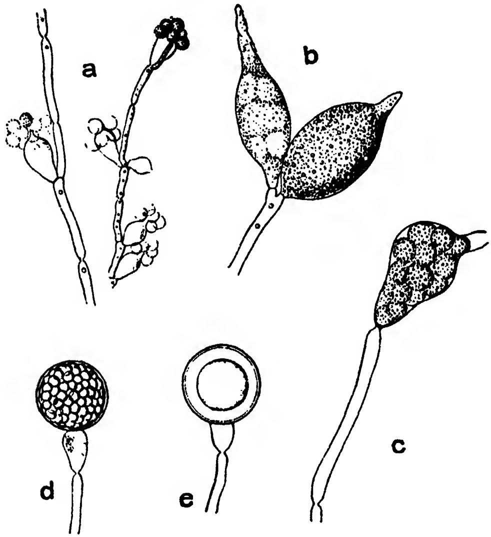

FIG. 65.—*Apodachlya pyrifera* (Zopf) Pringsheim. (*a*) Constricted hyphae bearing pyriform sporangia; swarmspores encysting as in *Achlya*. (*b*) Sporangia developed sympodially. (*c*) Sporangium with swarmspores. (*d*) Young resting spore. (*e*) Mature resting spore. (*After Zopf 1888.*)

3. **Sapromyces** Fritsch (1893; see also 1892).
   syn. *Naegelia* Reinsch (1878); see also Thaxter (1894).
   Naegeliella Schröter (1893).

In this genus the thallus is differentiated into a trunk and branches, but the trunk corresponds in shape with the branches and is of only slightly greater diameter. It is attached at its base to the substratum, rhizoids being poorly developed or even absent. The branches are definitely constricted at intervals, secondary branches arising at the apices of the segments. A spreading thallus results which is often extensive. The sporangia

are clavate to nearly cylindrical, arise at the apices of the segments and appear single or in whorls. The zoospores are apparently monoplanetic, and usually escape directly through a terminal

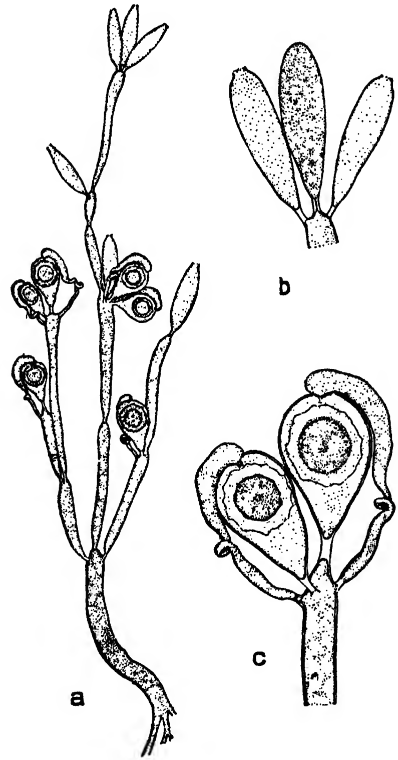

FIG. 66.—*Sapromyces androgynus* Thaxter. (*a*) General habit of small plant bearing sexual organs and swarmsporangia. (*b*) Swarmsporangia. (*c*) Two oogonia with oospores accompanied by antheridia on twisted branches. (*After Thaxter 1896.*)

pore. At times a tendency toward the formation of a thin-walled vesicle, such as that in *Rhipidium*, is noted, but the membrane ruptures early. The oogonium is typically pyriform, tapering to a narrowed base, and is separated from the hyphal segment by a

prominent cellulin plug. The oogonial wall is characteristically encrusted with a dark-colored flaky material. The antheridial branches are characteristically twisted. In *S. reinschii* (Schröter) Fritsch they are diclinous being long and winding, in *S. androgynous* Thaxter (Fig. 66) they are androgynous and short. These two species constitute the genus. The antheridium is terminal, and sends a fertilization tube to the solitary spherical oosphere.

4. **Araiospora** Thaxter (1896: 326).

In *Araiospora* the thallus is definitely tree-like (Fig. 67). A prominent cylindrical trunk of broad diameter is attached to the substratum by rhizoids, and bears at its apex a number of relatively slender cylindrical branches which in turn branch repeatedly in a definitely umbellate fashion. The branches are constricted at intervals, the secondary branches arising at the distal end of the segment. Two types of sporangia are formed, one smooth, the other more or less ornamented with spines or finger-like processes. The two differ also somewhat in shape and size, the smooth type tending to appear first and being the more slender. The genus at present contains three species, *A. pulchra* Thaxter, *A. spinosa* (Cornu) Thaxter, and *A. coronata* Linder (1926: 176). In the first two species the second type of sporangium is barbed over its surface with sharp spines. In *A. coronata* it is provided merely with a crown of finger-like processes at its apical end, and has somewhat the aspect of a basidium. Zoospore emergence occurs as in the preceding genus, a thin-walled vesicle being sometimes formed at the mouth of the sporangium and existing for a brief period. Oogonia and sporangia are often found associated, and both occur in whorls or umbels. They are separated from the hyphal segment by a definite constriction. The oogonium is spherical and monosporic. At maturity the oospore is surrounded by a layer of cell-like compartments which gives it a very characteristic aspect. Antheridal branches arise from special segments and may be branched. The antheridium is applied near the base of the oogonium. King (1903) studied *A. pulchra* in stained preparations and describes fertilization of a uninucleate oosphere as resulting from the entrance of a single antheridial nucleus. The genus is considered taxonomically by von Minden (1912: 588) and Kanouse (1927: 345).

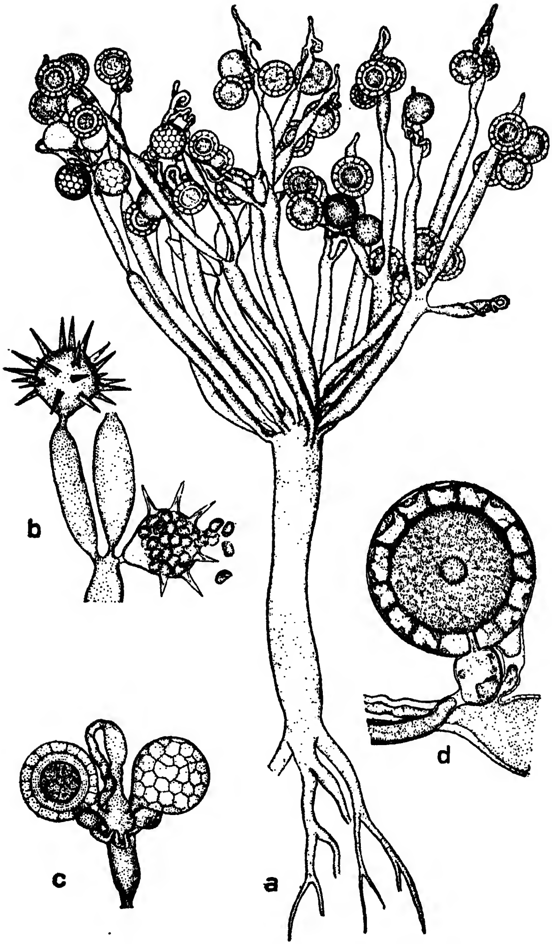

Fig. 67.—*Araiospora pulchra* Thaxter. (*a*) Plant bearing only oogonia and antheridia. (*b*) Segment bearing three sporangia, two of them spinose, the other smooth. (*c*) Two oogonia, one shown in optical section, the other in surface view. (*d*) Oogonium showing envelope of peripheral cells in process of formation. (*After Thaxter 1896.*)

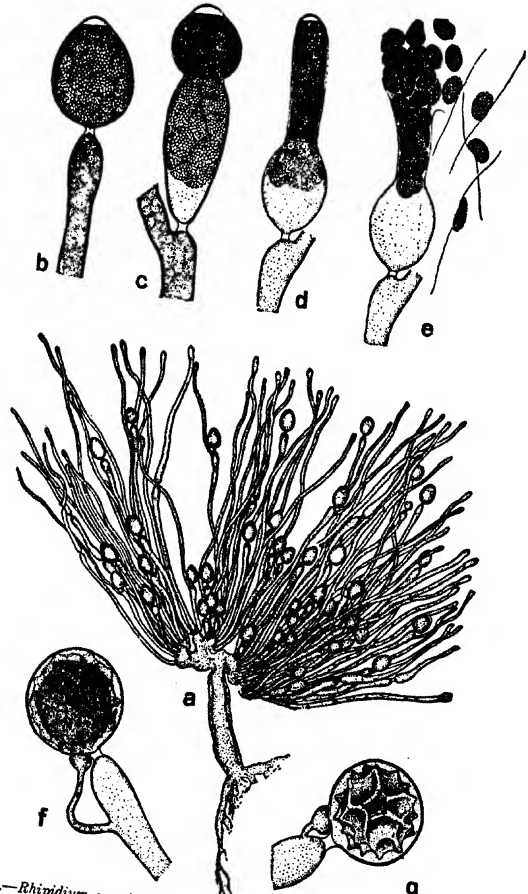

FIG. 68.—*Rhipidium americanum* Thaxter. (*a*) Typical plant, the branches showing occasional segmentation. (*b–e*) Sporangium with papilla of dehiscence extruding swarmspores into a thin-walled vesicle which finally ruptures freeing biciliate swarmspores. (*f*) Oogonium in which the exospore is being formed by the periplasm. (*g*) Mature oospore. (*After Thaxter 1896.*)

5. **Rhipidium** Cornu (*Bul. Soc. Bot. France,* **18**: 53, 1871).

In this genus, the basal segment of the thallus is attached to the substratum by rhizoids, and is often very irregular in form, being variously lobed or branched (Fig. 68). The lobes in turn give rise to numerous slender cylindrical branches which bear the sporangia and sexual organs. These slender branches are definitely constricted at their point of origin and elsewhere, especially in connection with delimitation of the reproductive cells. They may be sympodially branched below the originally terminal sporangia. The form of the sporangium varies in the different species from nearly spherical to long ellipsoidal, the cell being always markedly broader than the hypha which bears it. The zoospores pass from the sporangium into a thin-walled vesicle which tends to elongate and become cylindrical before rupturing. They are monoplanetic and reniform. The oogonium is usually borne terminally and is fertilized by an antheridium applied near its base. The oospore is prominently areolate at maturity. The genus contains at present four species, *R. americanum* Thaxter (1896: 320), *R. thaxteri* v. Minden (1912: 600), *R. europaeum* (Cornu) v. Minden (1912: 597), and *R. parthenosporum* Kanouse (1927: 344).

6. **Mindeniella** Kanouse (1927: 301).

The basal segment or main axis of the thallus in this genus is broadly club-shaped and essentially unbranched. Over its broadened distal end sporangia and oogonia occur on short pedicels. They are really sessile inasmuch as they are separated from the basal segment only by a constriction closed by a cellulin plug. The sporangium is large, pyriform to ovoid, and sometimes is ornamented with a circle of spines about the papilla of dehiscence. The oogonia appear after the sporangia have freed their zoospores. They are spherical, thick-walled, and spiny over the entire surface. The oospore is spherical, smooth-walled, and nearly fills the oogonium. Antheridia are unknown. The genus was based on a single species, *M. spinospora* Kanouse, and was referred by its author to the Blastocladiaceae. She states that zoospore formation is "as in the genus *Saprolegnia,*" but does not say definitely that biciliate spores are formed. The membranes are composed of true cellulose. Knowledge of the genus is confined entirely to the original description and figures.

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CHAPTER VIII

PERONOSPORALES

The highest point of development attained in the Oomycetes is reached in this order. The aquatic habit typical of the Saprolegniales and other lower forms has been largely abandoned, and most of the higher members of the order lead a terrestrial existence as parasites in the tissues of higher plants. Correlated with this change in habit has occurred a pronounced alteration in the character of the asexual stage. The **sporangia** are typically deciduous, and in the highest genera of the order germinate directly by germ tubes instead of by swarmspores. In general they are borne in the air on specialized hyphae termed **sporangiophores,** and are commonly disseminated by the wind. In the lower members of the group they usually germinate by swarmspores, though in some cases the type of germination is dependent on environmental factors. In a few of the most primitive forms, they develop under aquatic conditions and remain attached. When swarmspores occur they are of the reniform, laterally biciliate type.

The term **conidium** is applied by many writers to the sporangium in this group, but usage is extremely varied. Some authors prefer the term sporangium in all cases in which germination is by swarmspores. Others use conidium wherever the cell is deciduous, regardless of the method of germination. It is clear that from the morphological and phylogenetic points of view only a single structure is present, and the writer has found it desirable for the sake of clarity and uniformity of usage to avoid the application of the term conidium in the Oomycetes.

Mycelium is profusely developed throughout the entire order, and consists of more or less cylindrical, repeatedly branched hyphae of relatively small diameter as compared with those of the Saprolegniales. Septa are usually absent but may form in old hyphae. The mycelium of parasitic species is usually **intercellular,** the host cells being entered only by short lateral branches **termed haustoria.** These differ in form in the various genera,

being globose knobs in *Albugo* and elongate branching threads in *Peronospora*. In some cases (*e.g.*, *Phytophthora*) the mycelium may be also **intracellular,** the hyphae entering and passing directly through the host cells. Species characterized by intercellular mycelium are usually **obligate parasites,** while those with intracellular hyphae exhibit **facultative parasitism** and tend to develop well in artificial culture media. In some species the mycelium is perennial in the host, hibernates in the roots, and results in systemic infection of the parts above ground in the spring.

Oogonia and **antheridia,** resembling in general those of the preceding order are formed, but here they seem to be functional in all cases. The content of the oogonium is differentiated at maturity into a peripheral zone of protoplasm (**periplasm**) and a single central oosphere. After fertilization the **oosphere** is transformed into an **oospore,** the oogonium being monosporic throughout the group. The oospore usually lies free in the oogonium. It germinates in some forms by swarmspores, in others by a germ tube.

The order, Peronosporales, as here constituted, contains three families, Albuginaceae, Pythiaceae, and Peronosporaceae. The Pythiaceae are clearly the most primitive of the forms included, and were incorporated by Schröter (1893) in the Saprolegniales.

Key to Families of Peronosporales

A. Sporangia borne in a chain at the apex of a short, clavate, usually unbranched sporangiophore. Sporangiophores forming a limited sorus beneath the host epidermis, and exposed by its rupture.
1. **Albuginaceae,** p. 186

B. Sporangia usually borne singly at the tips of a branching sporangiophore, sometimes intercalary, rarely in chains. Sporangiophores not forming a sorus within the host.
1. Sporangiophore usually not sharply differentiated from the hyphae of the mycelium. Sporangia borne successively.
2. **Pythiaceae,** p. 193

2. Sporangiophore sharply differentiated from the hyphae of the mycelium, and bearing the sporangia simultaneously at the tips of its branches.
3. **Peronosporaceae,** p. 210

Albuginaceae

The members of this family occur as parasites on flowering plants, and, as far as is known, their parasitism is in all cases

obligate. The mycelium is strictly intercellular except for the production of small knob-like haustoria which lie just within the host cells. The sporangiophores are short, broadly clavate, and usually unbranched (Fig. 69). They are developed in a compact group just beneath the epidermis, and form there a definite palisade layer. At the tip of each sporangiophore sporangia are abstricted in basipetal succession, and remain attached forming a chain. The outward growth of these chains exerts sufficient pressure to rupture the epidermis, and an open sorus resembling that of the caeoma stage of certain rusts, except in color which is here white, results. Early investigators called the members of the family "white rusts." A superficial resemblance to the rusts is noted not only in the aspect of the sori, but also in the striking similarity of the chains of sporangia to chains of aecidiospores. Even an intercalary cell seems to be present between each pair of sporangia in the chain. This appearance is, however, an illusion resulting from the gelatinization of the outer layer of the walls of the sporangia at their point of contact, with the consequent formation of a small gelatinous disc between them. Complete gelatinization of the disc results in the falling apart of the sporangia. True intercalary cells such as exist in the rusts are absent. Though the sporangia tend to hang together for a time in rather long chains, they finally separate and form a dry white powder easily disseminated by the wind. The sporangium germinates by means of swarmspores.

The sexual organs are formed in the intercellular spaces of the host. The oogonium is globose and develops from a terminal or intercalary swelling of the mycelium. Its contents are clearly differentiated into a peripheral zone of periplasm and a single central spherical oosphere. The antheridium is clavate, and applies itself to the side of the oogonium. A fertilization tube enters the oogonium, reaches the oosphere, and ruptures, introducing one or more male nuclei. A true fertilization occurs, and a single oospore is matured. Germination of the oospore is by swarmspores.

The limits of the family are sharply defined, there being no close relatives in neighboring groups. The development of the sporangia in chains in a definite sorus beneath the surface of the host furnishes a striking point of difference between this group and the two other families of the order. While more highly developed in certain respects than the Pythiaceae it is

here treated first, since a position between the Pythiaceae and Peronosporaceae would fail completely to indicate the natural relationships.

The members of the family are all embraced in the single genus *Albugo*.

1. **Albugo** (Persoon) Gray (1821: 540).
   syn. *Cystopus* Lév. (1847: 371).

About twenty-five species have been described in this genus for the world. Wilson (1907 *a*; 1908 *a*) in his monograph of North American forms includes fifteen. Several of these are common

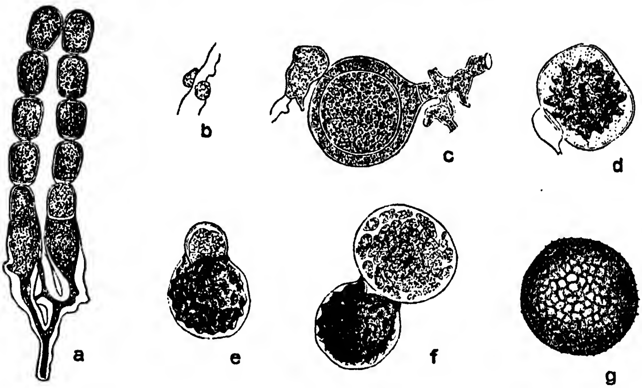

FIG. 69.—(*a*) *Albugo portulacae* (DC.) Kuntze, showing sporangiophores and chains of sporangia. (*b–f*) *A. candida* (Pers.) Kuntze. (*b*) Swarmspores. (*c*) Young oogonium and antheridium. (*d*) Mature oospore in oogonium. (*e–f*) Germinating oospore. (*g*) *A. tragopogonis* (DC.) Gray; mature oospore. (*g, after Schwarze 1917; others after de Bary 1887.*)

and almost cosmopolitan in distribution. The species may be separated into two groups on the basis of the character of the markings of the outer wall of the oospore (Fig. 69). Some (*e.g.*, *A. candida*, *A. ipomoeae-panduranae*) have a definitely tuberculate epispore, while in others (*e.g.*, *A. bliti*, *A. tragopogonis*, *A. portulacae*) it is reticulate. Cytological studies have demonstrated that differences in life-histories are correlated with this difference in epispore markings, the group characterized by the tuberculate epispore containing the more highly developed species. This fact will be clearly indicated in the following discussion of the sexual process.

The sexual organs of *Albugo*, on account of their hidden position in the interior of the host, were discovered much later than the sporangia. They were first noted by de Bary in *A. candida*. He saw the penetration of the fertilization tube to the oosphere, but, failing to observe its rupture, felt that it effected fertilization by contact only. His view was doubtless influenced by his earlier work on *Saprolegnia* where he had found parthenogenetic species. Subsequently, other investigators, using modern cytological technique, have examined *A. candida* and several other species of the genus, and have found a true sexuality in all. Their discussions indicate such a great diversity in the details of the sexual process in the different species that the genus must be regarded, from the standpoint of the cytologist, as one of the most remarkable and interesting in all the fungi. It will be necessary to summarize the results on several forms in order to give a clear conception of the situation in the genus as a whole.

In all of the species the young sexual organs are cut off by transverse septa from the main body of the hypha after the flowing in of the cytoplasm and nuclei. Both organs are multinucleate from the beginning. At about the time that the antheridium comes in contact with the oogonium a differentiation of the protoplasm of the latter into a peripheral zone of periplasm and a central spherical oosphere begins to take place. The majority of the nuclei are left within the limits of the oosphere.

In *A. candida* the oogonium contains approximately one hundred nuclei, the antheridium six to twelve, and these undergo one simultaneous division throughout both organs before the oosphere is formed. At the point of contact of the oogonium and antheridium the wall becomes very thin, and the oogonium pushes through forming a slight prominence within the antheridium. This has been termed the **receptive spot** (Wager, 1896 *b*) or the **receptive papilla** (Stevens, 1899; 1901). It seems to be functionless, and its formation may be due merely to the existence of a higher state of turgor in the oogonium than in the antheridium. It soon disappears, and the fertilization tube from the antheridium enters through the resultant thin spot in the wall, and advances to the oosphere. After completion of differentiation of the protoplasm of the oogonium into periplasm and ooplasm all of the nuclei, both in the antheridium and in the ooplasm, undergo a second mitosis, while those in the periplasm remain inactive and soon disorganize. Coincident with this second

mitosis a sphere of dense, deeply staining, slightly granular cytoplasm, several times the diameter of a single nucleus, appears in the center of the ooplasm. This structure has been termed the **central body** or **coenocentrum.** It is sometimes surrounded by a zone of lighter staining ooplasm through which delicate astral radiations pass. Though not a permanent structure in the cell it is prominent for a period immediately preceding fertilization. Shortly after its appearance a single female nucleus is attracted by it to the center of the oosphere and remains there while the other nuclei of the oosphere pass out into the periplasm where they form a sphere about the ooplasm. The fertilization tube carrying a single male nucleus and a small amount of cytoplasm then penetrates to the center of the oosphere, reaches the coenocentrum, and ruptures. The male nucleus comes in contact with the female nucleus and fuses with it, the fertilization tube collapses, is withdrawn from the oosphere leaving a large vacuole, and the wall of the oospore is laid down. The **endospore** is thin; the **exospore** is thick and at completion definitely tuberculate. The supernumerary nuclei in the antheridium and in the periplasm disintegrate following fertilization, and the coenocentrum disappears. The fusion nucleus soon divides and repeated mitoses result in the formation of about thirty nuclei. Since the number of uninucleate zoospores formed later in germination is slightly in excess of one hundred, Wager regards the thirty nuclei as spore-mother nuclei, and feels that they undergo the maturation divisions immediately before swarmspore formation. There is, however, as much reason to regard the two simultaneous mitoses which occur in the gametangia preceding fertilization as the reducing divisions; or from analogy with other fungi the first two mitoses of the fusion nucleus may well be regarded as accomplishing reduction. In any case in the absence of more complete knowledge only speculation is possible.

In *A. bliti* a wholly different type of fertilization has been described. In this species the oogonium contains about three hundred nuclei, and the antheridium about thirty-five. The receptive papilla extends far into the antheridium, and is much more prominent than in *A. candida*. As the content of the oogonium begins to differentiate into ooplasm and periplasm all of the nuclei migrate to the periphery undergoing a mitosis as they pass outward. Soon they are arranged in a hollow sphere

bordering the ooplasm. A section through the oogonium at this stage shows the vacuolate periplasm at the periphery, a circle of nuclei next within in the later stages of mitosis, and at the center the sphere of homogeneous ooplasm. Stevens calls this the stage of **zonation.** The division figures of certain of the nuclei in this division lie across the line of demarcation between the periplasm and the ooplasm, and in the completion of these divisions, one daughter nucleus in each case enters the ooplasm. Thus approximately fifty nuclei enter the oosphere. It becomes consequently a coenocytic structure and is termed by Stevens the compound oosphere. The nuclei in the antheridium divide simultaneously with those in the oogonium, resulting there in about seventy at this stage. The receptive papilla ruptures or is withdrawn, and the fertilization tube enters the oogonium and penetrates to the oosphere. A relatively small and inconspicuous coenocentrum is developed, but fails to function in attracting the sex nuclei, and disappears before fertilization occurs. A second division of all the nuclei in the antheridium and oosphere now takes place. Those in the periplasm fail to divide and soon disintegrate. This division results in the presence of about one hundred nuclei in the oosphere and one hundred and forty in the antheridium. The fertilization tube then ruptures, and the majority of the antheridial nuclei pass into the oosphere where the male and female nuclei fuse in pairs, approximately one hundred fusion nuclei resulting. The supernumerary male nuclei disintegrate, and the oospore wall is formed, the epispore being strongly reticulate. The multinucleate oospore then hibernates, the fusion nuclei passing the winter without change.

Reviewing the situation we see that in *A. candida* a single male nucleus fuses with a single female nucleus in a uninucleate oosphere, the receptive papilla is small, the coenocentrum is highly developed, the fusion nucleus divides rapidly to form about thirty nuclei before hibernation, and the epispore is tuberculate. In *A. bliti* many male nuclei fuse in pairs with female nuclei in a multinucleate oosphere, the receptive papilla is long and prominent, the coenocentrum is relatively inconspicuous and functionless, the fusion nuclei do not divide before the period of rest, and the epispore is reticulate.

The sexual process in *A. portulacae* is very similar to that in *A. bliti*, while that in *A. lepigoni* (Ruhland, 1903) is practically

identical with that in *A. candida.* In *A. tragopogonis* a multinucleate oosphere develops as in *A. bliti,* but while all the nuclei in the oosphere may be termed potentially sexual, they are not all functional. Following the two divisions in the oogonium, resulting in a multinucleate oosphere, all but one of the nuclei disorganize. The antheridium empties several nuclei into the oosphere, but all but one of these also disorganize. The remaining pair of nuclei fuse. The fusion nucleus undergoes repeated divisions at once, the oospore entering the winter in the multinucleate condition. The coenocentrum is almost as highly developed as in *A. candida,* but the receptive papilla is relatively inconspicuous. In *A. ipomoeae-panduranae* there are apparently a few supernumerary female nuclei which disintegrate in the oosphere, but the fertilization tube discharges only a single male nucleus. Stevens regards the multinucleate condition in *A. bliti* and *A. portulacae* as primitive, and the uninucleate condition in *A. candida* as a higher development. Arranging the species in a series and passing from *A. portulacae* at one extreme to *A. candida* at the other it will be noted that the coenocentrum increases in height of development and the receptive papilla decreases in size as the number of functional sex nuclei passes from many to one and the epispore changes from reticulate to tuberculate.

The species enumerated below are the common representatives of the genus in North America. For technical descriptions the papers of Wilson (1907 *a*; 1908 *a*) should be consulted.

A. candida (Pers.) Kuntze—On many genera and species of the mustard family; probably best known on shepherd's purse (*Capsella*).

A. bliti (Biv.) Kuntze—Common on various species of *Amaranthus* (pigweed) and on a few related plants.

A. ipomoeae-panduranae (Schw.) Swing.—On various Convolvulaceae. The form on *Ipomoea batatas* has been named *A. minor* (Speg.) Cif. (Nuovo. Gior. Bot. Ital. n. s. **35**: 132, 1928.)

A. portulacae (DC.) Kuntze—Restricted to the common purslane, *Portulaca oleracea* L.

A. tragopogonis (DC.) S. F. Gray—Attacking a wide variety of Compositae (common on ragweed, Canada thistle, and salsify).

Recently Wakefield (1927) has revived the name *Cystopus,* and applies it to the genus in preference to *Albugo.* She does this in an attempt to follow the International Rules of Nomenclature (art. 49 bis), which state that, in the case of fungi having a pleomorphic life cycle, only names applied to the perfect stage

may be recognized. Since the oospores of this genus were first described by de Bary (1863) under the name *Cystopus* she attributes the genus to him rather than to Léveille who first used the name *Cystopus* for the sporangial stage alone.

The wording of the rule is such as to leave open to question the necessity of its application to the Phycomycetes, and in other respects its meaning is not clear. Some workers (*e.g.*, Murphy 1918) have interpreted it as excluding the Phycomycetes. Until it is further elucidated the writer prefers to retain the name *Albugo*, now well established in the American literature.

Pythiaceae

The members of this family are clearly the most primitive of the Peronosporales, and in certain respects stand as an intermediate group between the Saprolegniaceae and Leptomitaceae on the one hand, and the Peronosporaceae on the other. In the lower members of the group the habit is aquatic, the sporangia remain attached, and swarmspores constitute the usual method of asexual propagation. In the higher members the habit is terrestrial, the sporangia are deciduous, and germination is sometimes by germ tube. Intermediate species exemplify intermediate conditions. Parasitism is less highly developed throughout the group than in the Peronosporaceae, and apparently is never obligate. In some of the most highly developed forms (*e.g.*, *Phytophthora infestans*) a definite sporangiophore is developed, but in most cases the hyphae which bear the sporangia are not sharply differentiated from those of the vegetative mycelium. Even when a specialized sporangiophore is present it does not mature its sporangia simultaneously at the tips of its branches as in the Peronosporaceae. Instead, they are developed successively, sporangia of different ages existing together on the same sporangiophore. Moreover, the sporangiophore may develop extensively even after some of the sporangia have reached maturity. The mycelium in the Pythiaceae is of small diameter (3–4μ, rarely 7μ), is abundantly and irregularly branched in most species, and may be septate at maturity. (See Jour. Agric. Res. **40**: 557, for "diplanetism.")

The family was placed by Schröter (1893) in the Saprolegniales, but most authors have included it in the Peronosporales. Its intermediate character has rendered difficult the task of finding a satisfactory basis for a taxonomic separation of the

two orders. On the one hand, the highest of the Pythiaceae provide a series of closely intergrading forms connecting the family with the Peronosporaceae, while on the other, the lowest of the Pythiaceae are so similar in various respects to members of the Saprolegniales that the two groups tend to merge at the border line. The sexual stage corresponds to that of the Peronosporaceae rather than to that of the Saprolegniaceae, but does not differ essentially from that of the Leptomitaceae. In general, the mycelium corresponds to that of the Peronosporaceae in its small diameter and tendency to irregularity.

Key to Genera of Pythiaceae

I. Sporangium much broader than the mycelium, strikingly asymmetrical in form, and standing usually with its long axis at right angles to that of the sporangiophore.

1. **Pythiogeton**, p. 194

II. Sporangium not standing with its long axis at right angles to that of the sporangiophore, in most species broader than the mycelium and symmetrical (oval, spherical, obpyriform, etc.), in a few cases (subgenus *Aphragmium* of *Pythium*) filamentous.

A. Sporangial wall smooth.

1. Sporangium, in germination, discharging the swarmspores in an imperfectly differentiated state into a thin-walled vesicle, which later ruptures allowing the fully formed spores to escape.

2. **Pythium**, p. 195

2. Swarmspores sometimes discharged fully formed into a vesicle, but usually freed directly through a pore in the sporangial wall.

3. **Phytophthora**, p. 199

B. Sporangial wall echinulate; germination by germ tube; swarmspores unknown.

4. **Trachysphaera**, p. 209

1. Pythiogeton v. Minden (1916: 228).

This genus includes three species, *P. utriforme*, *P. transversum*, and *P. ramosum*, all of them described by von Minden. It is closely related to *Pythium*, differing chiefly in that the sporangium has the aspect of being attached at its side to the sporangiophore instead of at its base. The long axis of the sporangium lies at a right angle to that of the sporangiophore, and germination takes place at one end of this axis instead of opposite the point of attachment (Fig. 70). In germination, the undifferentiated plasma of the sporangium flows into a thin-walled, tubular,

often much elongate vesicle, accumulates at its tip, and at its rupture passes as an undifferentiated mass into the water, finally breaking up there into swarmspores. Proliferation of sporangia is of frequent occurrence. Their germination by germ tube is unknown. The branch bearing the oogonium is characteristically coiled around that bearing the antheridium. The oogonium is globose or polygonal, and is almost completely filled by the oospore which has a thick, hyaline, concentrically

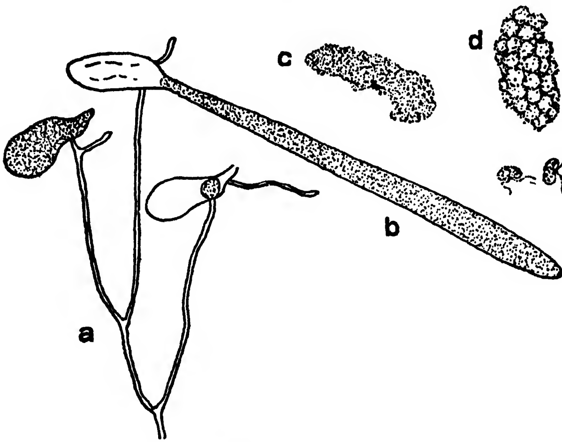

FIG. 70.—*Pythiogeton transversum* v. Minden. (*a*) Mycelium bearing three sporangia, one empty and another showing the extrusion of the contents into a tubular vesicle (*b*). (*c*) Undifferentiated plasma after rupture of vesicle. (*d*) Partially formed swarmspores. (*e*) Mature ciliated swarmspores. (*After v. Minden 1916.*)

stratified wall. The method of oospore germination is unknown. The mycelium is of small diameter and is saprophytic in vegetable substrata in the water.

2. **Pythium** Pringsheim (1858).

The genus *Pythium* was erected by Pringsheim on two aquatic species, *P. monospermum* Pringsheim and *P. entophytum* Pringsheim. The latter species was later transferred to *Lagenidium* of the Ancylistales by Zopf. In Pringsheim's account the genus is a member of the Saprolegniaceae, and as such was placed by him in the algae. Other species were soon discovered and described; *P. gracile* Schenk in 1859, *P. proliferum* de Bary in 1860,

P. cystosiphon (Roze & Cornu) Lindstedt in 1872, *P. debaryanum* Hesse in 1874, and *P. vexans* de Bary in 1876. The economic importance of the genus was first realized with the appearance of the paper of Hesse (1874). In 1881 de Bary transferred the genus to the Peronosporaceae, placed near it his own genus *Phytophthora*, and described several additional species, *P. ferax* de Bary, *P. megalacanthum* de Bary, *P. intermedium* de Bary, and *P. artotrogus* (Montagne) de Bary.

In 1892 Fischer followed de Bary in placing *Pythium* in the Peronosporaceae, but split the genus into three subgenera, *Sphaerosporangium*, in which the sporangia are typically more or less spherical, and *Aphragmium* and *Nematosporangium*, in which they are filamentous. As treated by him *Nematosporangium* embraces only a single species, *P. monospermum*, which he states differs from *Aphragmium* in that a septum cuts off the sporangium from the remainder of the hypha. In *Aphragmium* the sporangium is indeterminate in extent, a septum being lacking.

Schröter (1893) raised *Nematosporangium* to the rank of a genus, and extended its limits to embrace *Aphragmium*, thus leaving *Pythium* equivalent to *Sphaerosporangium* of Fischer. Moreover, he created a new family, Pythiaceae, to include the two genera and placed it in the Saprolegniales. In this manner, *Pythium* and *Phytophthora* came to lie in different orders, the latter genus being retained in the Peronosporaceae. The inclusion of *Pythium* in the Saprolegniales is clearly illogical, and Schröter's classification in this regard differs from those of other modern authors.

In 1907 Butler published a monographic treatment of *Pythium*, based on extensive research on the group in India, and presented a separation of seventeen species which has stood for twenty years as essentially satisfactory. Meanwhile, no other comprehensive discussion of the genus has appeared. In Butler's account *Nematosporangium* and *Aphragmium* are merged as one subgenus under the latter name, his monograph covering the entire genus *Pythium* as understood by Fischer.

In *Aphragmium* the sporangium is filamentous and often branched. It is evidently merely an indeterminate portion of the mycelium functioning as a sporangium. It is not separated from the remainder of the hypha by a septum, and portions of the protoplasm which remains may form other

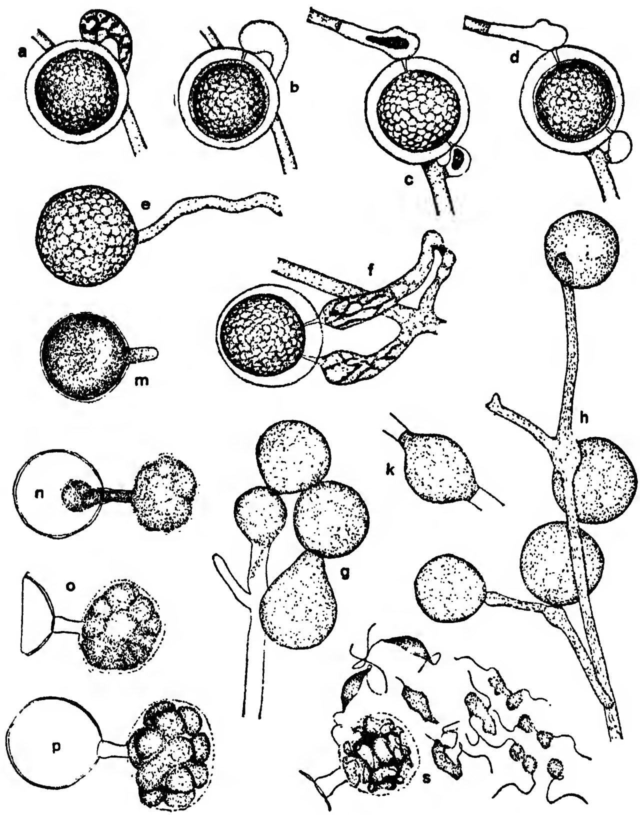

FIG. 71.—(*a–f*) *Pythium debaryanum* Hesse. (*g–s*) *P. intermedium* de Bary. (*a*) Oogonium with fully formed oosphere before fertilization. (*b*) Same after fertilization. (*c*) Oogonium before fertilization, accompanied by two antheridia in which differentiation into gonoplasm and periplasm has occurred. (*d*) Same after fertilization. (*e*) Young oogonium. (*f*) Oogonium with a pair of antheridia. (*g*) Chain of sporangia. (*h*) Sporangia formed successively and becoming lateral by further elongation of the hypha. (*k*) Intercalary sporangium. (*m–p*) Steps in phenomenon of extrusion of contents of sporangium into vesicle. (*s*) Swarmspore formation. (*After Atkinson 1895.*)

sporangia which discharge through other branches. The sporangia are thus terminal or intercalary, and ultimately may form throughout the entire mycelium. Here, as in the remainder of the genus, the swarmspores pass out incompletely differentiated into a spherical, thin-walled vesicle which later bursts allowing their escape. Germination of the sporangium by a germ tube has not been observed, *i.e.*, so called conidia are lacking. The antheridia and oogonia are cut off by septa except in a single species, *P. tenue* Gobi, where the septum is absent at least in the antheridial branch. As treated by Butler the subgenus includes, *P. tenue*, *P. gracile* Schenk, *P. monospermum* Prings., *P. indigoferae* Butler, and *P. dictyospermum* Racib. The fungus *Rheosporangium aphanidermatum* Edson (1915), cause of damping-off of beet seedlings has been shown to belong here (Fitzpatrick, 1923). It is stated by Carpenter (1921) to be the same as *P. butleri* Subramaniam (1919) which causes a disease of ginger, tobacco, papaya, and sugar cane. Also *P. afertile* Kanouse & Humphrey (1928), *P. graminicolum* Subramaniam (1928), *P. torulosum* Coker & Patterson (1927), and *P. arrhenomanes* Drechsler (1928) have been placed here, though in some of these the sporangium is too broad to be wholly typical of this subgenus.

The subgenus *Sphaerosporangium* contains a larger number of species. Butler recognizes thirteen, and others have been described since, including *P. irregulare* Buisman (1927), and *P. mamillatum* Meurs (1928). No paper has yet appeared giving a separation of all the described species.

The sporangium in *Sphaerosporangium* is usually spherical to ovoidal, but may have the obpyriform shape more typical of species of *Phytophthora*. It is cut off from the fertile hypha by a septum. Definite sporangiophores are lacking, the sporangia arising throughout the mycelium from undifferentiated hyphae. Though usually terminal the sporangia are sometimes intercalary, and may exist in chains. When developed in the air they may be deciduous, but when submerged usually remain attached. Germination takes place either by swarmspores or by germ tube, and in some species it is possible to predict one type or the other in cultures under controlled environmental conditions. The "conidia" of Butler and other writers are merely sporangia undergoing direct germination.

In swarmspore formation, as in *Aphragmium*, a thin-walled vesicle is extruded, and the protoplasm passes out into it before

the swarmspores are fully formed. The vesicle may arise at the apex or at the side of the sporangium. Frequently it is initiated as a cylindrical tube which may attain considerable length before becoming inflated at the tip to form a globose bladder. The recent use of the term **emission collar** by Sideris (1929) is in this connection. The swarmspores escape by the rupture of the vesicle, and are then seen to be reniform and laterally biciliate (not uniciliate as usually pictured for *P. debaryanum*). Some writers apply the term sporangium to the vesicle which frees the spores, and designate the primary cell from which it arises the **prosporangium** (**presporangium** of Edson, 1915). This terminology is confusing and in any case cannot be applied in the related genus *Phytophthora*, where in a given species the vesicle is sometimes formed and sometimes absent.

The oogonia and antheridia of species of *Pythium* are developed on either the intra- or extramatrical mycelium. The sexual process corresponds in general to that described for *Peronospora parasitica*. Differentiation into ooplasm and periplasm occurs, a coenocentrum is present, fusion of one male with one female nucleus takes place, and the oospore germinates usually by a germ tube. The details of the process are given by Trow (1901) for *P. ultimum*, by Miyake (1901) for *P. debaryanum*, by Patterson (1927) for *P. torulosum*, and by Edson (1915) for *P. aphanidermatum*.

The genus *Zoophagus* Sommerstorff (1911), based on *Z. insidians* Som., a species attacking rotifers, is apparently too close to the subgenus *Aphragmium* of *Pythium* to permit of its recognition as a separate genus. This species has been discussed by Arnaudow (1918; 1925), Gicklhorn (1922), Mirande (1920), and Sparrow (1929). The latter writer, basing his observations on American material, gives us a clear conception of the species. The fungus differs from *Aphragmium*, as thus far described, in possessing "gemmae" in addition to the filamentous sporangia. The swarmspores are said to be diplanetic, and the species is heterothallic.

3. **Phytophthora** de Bary (1876: 240).

Although most authorities on the Phycomycetes have included *Phytophthora* in the Peronosporaceae, it is here removed from that family and incorporated in the Pythiaceae because of the

indefinite character of its sporangiophore and the successive development of its sporangia. In these respects it differs strikingly from such genera as *Peronospora*, *Plasmopara*, and *Sclerospora*. Its close relationship to *Pythium* forbids the treatment of the two genera in different families as advocated by Schröter (1893). In fact the two genera stand so close together that at present no satisfactory basis for a generic separation is known (Fitzpatrick, 1923). The recognition of *Phytophthora* as a genus distinct from *Pythium* is chiefly in deference to precedent. The merging of the two genera under the older name *Pythium* will probably take place in time unless future research on the group reveals a more tangible basis for their separation than any known at present.

De Bary, in founding the genus *Phytophthora*, realized its close relationship with *Pythium*, but felt that the difference in sporangial germination existing in the species known to him served to separate the two. Butler (1907), the foremost student of the Pythiaceae, has accepted de Bary's point of view as a basis for retention of the two generic concepts. He emphasizes the fact that in *Pythium* germination is always accomplished by the extrusion of the contents of the sporangium into a thin-walled vesicle which finally bursts freeing the spores. Later work by Rosenbaum and others demonstrated that a vesicle is not infrequently formed in *Phytophthora*, though it is true that the swarmspores of this genus usually escape directly from the sporangium. When a vesicle is formed in *Phytophthora* the swarmspores are said to be fully formed before their migration into the vesicle begins. In *Pythium*, according to Butler, they flow out in an incompletely differentiated state and attain their final form in the vesicle. Unfortunately, the determination of the exact point at which the final fashioning of the swarmspores is accomplished often proves difficult if not actually impossible. Moreover, in at least one species (*Phy. palmivora* Butler) germination may be at times typical of *Pythium*, while at others a vesicle is absent and the swarmspores escape directly from the sporangium. It is clear that this character used alone provides at best an unsatisfactory separation of the two genera.

The shape of the sporangium in most species of *Pythium* may be said to be characteristically more nearly spherical than in *Phytophthora* where it is usually oval to obpyriform and papillate, but so many intergrading conditions exist that shape has only

relative diagnostic value. Buisman summarizes the situation with the statement that although theoretically no sharp line can

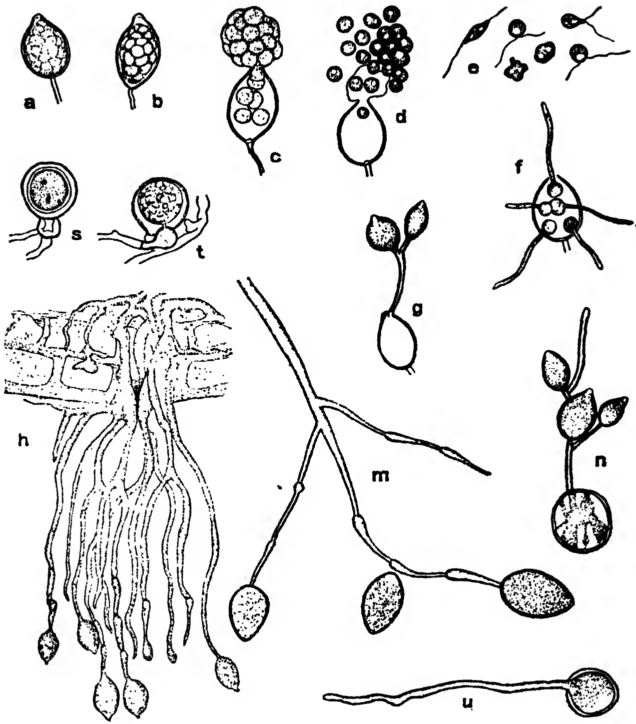

FIG. 72.—*Phytophthora spp.* (*a–e*) Germination of sporangium by swarmspores, the spores passing first into a vesicle. (*f*) Sporangiospores which failed to escape germinating by germ tubes in the sporangium. (*g*) Secondary sporangia developed at tip of germ tube of primary sporangium. (*h*) Sporangiophores of *Ph. phaseoli* arising from a stomate of lima bean. (*m*) Sporangiophore of *Ph. infestans.* (*n*) Oospore germinating by a germ tube on which sporangia then form. (*s*) Oogonium, basal antheridium, and oospore in *Ph. erythroseptica.* (*t*) Oogonium, lateral antheridium, and oospore in *Ph. cactorum.* (*u*) Germination of oospore by simple germ tube. (*h, after Thaxter 1889; m, after Schwarze 1917; others after Rosenbaum 1916, 1917.*)

be drawn between the two genera it is usually possible in practice to determine whether a given form belongs to the *Phytophthora* type or to the *Pythium* type.

The species included in *Phytophthora* are more typically parasitic in their natural habitat than those embraced in *Pythium*, but nearly all of them will grow on artificial culture media. In the host the hyphae are intra- as well as intercellular, and in the latter case bear haustoria. Usually on the host the branches which bear sporangia (Fig. 72) protrude from the stomates, but in culture they are developed indefinitely over the surface of the medium. Though these branches are termed sporangiophores they differ little if any from the vegetative hyphae. Their branching is sympodial in type, terminally produced sporangia coming to occupy a lateral position due to further apical growth of the hypha. The production of sporangia is thus successive and differs essentially from the simultaneous maturation of sporangia at the tips of a specialized sporangiophore as seen in the Peronosporaceae. In several species (*Phy. infestans*, *Phy. phaseoli*, *Phy. thalictri*) a slight thickening of the hypha occurs immediately below the point of attachment of the sporangium, and gives it a characteristic aspect, but this is absent in other species. Germination of the sporangium by means of one or more germ tubes may occur, and in some cases secondary and even tertiary sporangia may be formed on these tubes. When germination by swarmspores takes place a part or all of the spores may round up while still within the sporangium and germinate *in situ* by germ tubes. The sporangia developed in the air in nature fall away and are wind borne, but those developed in culture usually germinate while still attached to the sporangiophore. The term conidium is frequently encountered in the literature of this genus and has been applied to the sporangium without reference to its method of germination. Spherical, smooth, thick-walled, terminal or intercalary spores, usually yellowish or brownish in color, are sometimes found and have been termed chlamydospores. Investigators have interpreted them in different ways: as resting conidia, as parthenogenetic oospores, etc.

The sexual process in the genus is in one respect remarkable. Pethybridge (1913 *b*) demonstrated that in some of the species, designated by him the *infestans* group, the antheridium exists at maturity as a collar around the base of the oogonium. The oogonium is initiated beneath the antheridium, perforates its wall, passes into its interior, grows entirely through it, emerges at its summit, and swells out there to form the spherical portion in

which later the oospore develops. The mature sexual apparatus thus consists of a balloon-shaped oogonium with a thick-walled oospore in its upper swollen portion and with its funnel-shaped base within and surrounded by the antheridium. Murphy studied cytologically a member of this group, *Phy. erythroseptica*, and demonstrated that, following the protrusion of a receptive papilla (**manocyst**) into the antheridium, a fertilization tube enters the oogonium and discharges into it a single male nucleus which later fuses with a nucleus in the oosphere. In other species of the genus, designated the *cactorum* group, sexual organs of the usual oomycetous type are developed, the antheridium being applied more or less laterally and sending into the oogonium a fertilization tube as in *Pythium*. Pethybridge, impressed by the unique type of sexuality in the *infestans* group, split the genus *Phytophthora* into two and applied the generic name *Nozemia* to the members of the *cactorum* group, retaining *Phytophthora* for the *infestans* group because he regarded *Phy. infestans* as the type species of the genus. Wilson went even farther and suggested the recognition of a new family Phytophthoraceae and a new order Phytophthorales for the *infestans* group. Since the sporangial stage is wholly similar in the two groups, and since this vagary of the sexual process constitutes the only difference between them, the splitting of the genus was questionable and proved to be premature. Later Lafferty and Pethybridge found that in some species both basal (**amphigynous**) and lateral (**paragynous**) antheridia are produced. The separation of the groups, therefore, can no longer be justified and *Nozemia* has been abandoned. Species in which the basal type of antheridium is known include *Phy. infestans*, *Phy. phaseoli*, *Phy. erythroseptica*, *Phy. parasitica*, *Phy. arecae*, *Phy. cryptogea* and others Only the lateral type has been observed in certain others.

Although the observations of Pethybridge concerning the penetration of the antheridium by the oogonium were at first received with scepticism, the observations of other workers and in particular the cytological study by Murphy (1918) have corroborated his statements. Moreover, Tabor and Bunting (1923) have described and figured the same phenomenon in a new genus, *Trachysphaera* Recently Rose and Lindegren (1925) have figured for *Phy. cactorum* oogonia bearing both amphigynous and paragynous antheridia; and one oogonium bearing two

amphigynous antheridia is pictured. Such cases have not yet been explained. The latter case would appear to be inexplicable in the light of Murphy's account, and the question is raised whether the amphigynous antheridium has that position because the oogonium has grown through it or for some other reason such as the coiling of the antheridium around the base of the oogonium (Cooper, 1928; Cooper & Porter, 1928). No cytological evidence has been advanced to refute the observations of Murphy, who in the study of serial sections, found the base of the oogonium within the antheridium.

A satisfactory basis for separation of species within the genus *Phytophthora* has not yet been found. Many species have been described, but the identification of an unknown form is often difficult if not actually impossible. A number of specific names at present applied will doubtless in time be placed in synonymy. Tangible morphological characters are few and variable, while separations based on host relationships and cultural characters have proved inadequate. A thorough taxonomic revision of the genus and its close relatives is now imperative.

Considerable taxonomic work has been done on the genus by Rosenbaum (1915; 1917) and Leonian (1925). The former author presents a key separating eleven species. In his studies he uses biometrical methods, and bases his spore and sporangial measurements on the examination of hundreds of individuals. His method, while perhaps sound, is extremely laborious in application. Leonian presents a key separating eighteen species on cultural characters. The presence or absence of sporangia or oogonia on specified media afford the basis for separation. Leonian (1927) also states that remarkable modifications in the morphology of the sporangium take place when a given species is grown on various hosts. He concludes that material taken directly from the host for identification is less desirable than that developed under controlled cultural conditions in the laboratory. More recently Leonian and Geer (1929) have made a comparative study of the size of sporangia in many species, and conclude that many specific names now used must be thrown into synonymy. Workers in general have stressed host relationships in delimiting species, and in a number of cases new species have been erected, chiefly because new hosts were involved.

In no published paper have all the described species been discussed together. At present thirty or more species exist in

the literature. It is hoped that the following resumé will serve to put the reader in touch with the general situation.

Phytophthora infestans (Mont.) de Bary (1876) is the cause of the widely disseminated and extremely destructive late blight of potato, and, from the economic standpoint, is the outstanding species of the genus. It is now found wherever the host is grown. The early home of the potato is not certainly known. When first introduced into Europe it was apparently free from the blight but later the disease appeared there in epiphytotic form, and two outbreaks, one in 1845 (cause of the Irish Famine) and another in 1875 are now historical. In the latter year the celebrated German mycologist Anton de Bary undertook the study of the disease, and the publication (1876) of his results constitutes the first paper of importance on any species of the genus. In it he erects the genus *Phytophthora* on this species. He describes the sporangial stage, but did not find oospores. He states that the fungus hibernates in the tuber in the mycelial condition, and grows up through the young shoots the following spring giving a systemic infection of the plant above ground. The English mycologist, Worthington G. Smith (1875; 1876 *a*, *b*, *c*) described and figured the oospores stating that he had discovered them in the leaves. His observations were not substantiated by others and his account fell into disrepute. For many years mycologists regarded the species as lacking the sexual stage. Finally Clinton (1911 *a*, *b*) announced that he had obtained oospores in pure culture on oat agar, and others have since succeeded in duplicating his results (Brüyn, 1923). Clinton also obtained hybrid oospores between mycelia of *Phy. infestans* and *Phy. phaseoli* Thaxter. More recently Murphy (1927) has found oospores on the surface of tubers in nature The species is not confined to the potato. It occurs also on tomato, eggplant, and other solanaceous hosts. According to Berg (1926) the fungus on tomato is a different biological strain from that on potato. Important papers on the species have been published by Jones (1912), Clinton (1905 *b*; 1906 *a*), Melhus (1915 *b*), and Pethybridge (1911 *a*; 1912; 1913 *c*). Although *Phy. infestans* is grouped with the species characterized by amphigynous antheridia, the oospores are in fact usually developed in the complete absence of antheridia. The spores are then termed by some authors chlamydospores.

Phytophthora phaseoli Thaxter (1889) parasitic on the lima bean, *Phaseolus lunatus*, is fully treated by Clinton (1906 *b*).

The fungus attacks the pod especially, producing a woolly white growth of sporangiophores over its surface (Fig. 77, *c*). The oospores are developed in the seed of the host. Leonian (1925) regards the species as a variety of *Phy. infestans*.

Phytophthora omnivora de Bary (1881) represents the merging and treatment under a new name of three previously described species. These include *Peronospora cactorum* Lebert & Cohn (1871), described as causing a rot in two species of cactus, *Peronospora fagi* Hartig (1876), cause of damping-off of beech seedlings, and *Peronospora sempervivum* Schenk (1875), parasitic on *Sempervivum*. The new specific name *omnivora* was used by de Bary without regard to priority, and alludes to the occurrence of the species on many hosts. Schröter (1889) revived the older name *cactorum*, and is responsible for the binomial, *Phytophthora cactorum* (Lebert & Cohn) Schröter. At present, in the absence of uniformity of opinion concerning specific limits, *Phy. cactorum*, *Phy. fagi*, and *Phy. omnivora* may be found in the literature treated as distinct species or merged in various ways with each other or with still other forms. Leonian (1925) recognizes *Phy. omnivora*, but merges with it *Phy. colocasiae*, *Phy. palmivora*, *Phy. faberi*, *Phy. parasitica*, *Phy. terrestria*, and *Phy. parasitica* var. *rhei*, while recognizing *Phy. cactorum* as a distinct species. In England a rot of apples and pears is attributed by Wormald to *Phy. omnivora*. Drechsler states that the species is the cause of a foot rot of lilies, and other authors report it on ginseng (Rosenbaum, 1915), strawberries, rhubarb, and other plants.

Phytophthora palmivora Butler (1919) cause of the well known bud rot of Palmyra palms in India is, perhaps, not specifically distinct from *Phy. meadii* McRae (1918 *a*, *b*) and *Phy. faberi* Maublanc (1909) reported from *Hevea* (rubber), cocoa, coconut, and other tropical plants. See Gadd (1927).

Phytophthora erythroseptica Pethybridge (1913 *b*; 1914) causes a pink rot of potato tubers and has been reported from Ireland, England, Holland, Switzerland, and Java.

Additional published species are *Phytophthora agaves* Gandara (1909), *Phy. allii* Sawada (1915), *Phy. arecae* Pethybridge (1913 *b*), *Phy. capsici* Leonian (1922), *Phy. carica* (Hara) Hori (in Sawada, 1919), *Phy. citri* Rau (1916), *Phy. cinnamomi* Rand (1922), *Phy. cryptogea* Pethybridge & Lafferty (1919), *Phy. colocasiae* Raciborski (1900), *Phy. fici* Hori (1915 in Japanese: see Sawada,

1919), *Phy. hibernalis* Carne (1927), *Phy. hydrophila* Curzi (1927), *Phy. jatrophae* Jensen, *Phy. lepironiae* Sawada (1919), *Phy. melongenae* Sawada (1915), *Phy. mexicana* Hotson & Hartge (1923), *Phy. nicotianae* Breda de Hahn (1896), *Phy. paeoniae* Cooper & Porter (1928), *Phy. parasitica* Dastur (1913), *Phy. pini* Leonian (1925), *Phy. richardiae* Buisman (1927), *Phy. syringae* Klebahn (1909), *Phy. thalictri* Wilson & Davis (in Wilson, 1907 *b*), and *Phy. theobromae* Coleman (1910).

Several genera have been erected on species which do not seem to differ generically from *Phytophthora*. One of these, *Pythiacystis* Smith & Smith (1906: 221) was founded on the causal organism of the destructive brown rot of lemon, *Pyth. citrophthora* Smith & Smith, and has remained monotypic. The sexual stage of the organism has not been observed, but the characters of its mycelium and sporangia show it to be intermediate in many respects between *Pythium* and *Phytophthora;* the habit being as in the former and the morphology as in the latter in as far as differences may be said to exist. The mycelium in the parasitic phases on the host plant is always sterile. In the soil or in soil water sporangia occur in abundance. Definite sporangiophores are not formed. The sporangia germinate by swarmspores or by germ tubes, in the former case delimitation taking place in the sporangium and a vesicle being absent. The sporangia are frequently asymmetrical, and two or more papillae of germination are sometimes formed. The authors of the genus and others (Barrett, 1917; Leonian, 1925) have concluded that the species may well be incorporated in *Phytophthora*. Leonian has recently made the transfer, and the name now stands, *Pyth. citrophthora* (Smith & Smith) Leonian.

The genus *Kawakamia* Miyabe (1903: 306) was established in Japan on a single species, *K. cyperi* (Miy. & Ideta) Miyabe, found on *Cyperus*. A second species, *K. carica* Hara, on *Ficus carica*, was described later, and *Phytophthora colocasiae* Racib. was transferred to the genus by Sawada (1919). The author of the genus regarded it as differing from *Phytophthora* in that the sporangium in falling away carries with it a small portion of the sporangiophore. He regarded this as a separate cell and termed it the **pedicel cell.** The sporangiophore was stated by him to be unbranched or only slightly and indefinitely branched. As the original account was inadequate, Sawada (1919) reinvestigated the species, and gives figures which show the genus to agree

essentially with *Phytophthora*. The sporangiophore branches as in that genus, and sporangia arise successively. The pedicel cell is regarded by Sawada (in Tanaka, 1920) as being merely a thickening of the wall at the basal end of the sporangium. Earlier Wilson (1914 *b*) had treated *Kawakamia* as a well defined genus showing relationship with *Basidiophora*. The writer feels that there is no basis for separating it from *Phytophthora*.

The genus *Blepharospora* Petri (1918; 1924) was founded on *B. cambivora* Petri, cause of the inky spot disease of chestnuts in Italy. The species is said by Petri to possess a long, unbranched sporangiophore terminated in a single sporangium. Further, the sporangiophores are said to develop only in a liquid medium. Peyronel (1920) transferred *Phy. terrestria* Sherbakoff to the genus as *B. terrestris* (Sherb.) Peyronel. Other species of *Phytophthora* are closely related to it. Buisman (1927) advocates the merging of *Blepharospora* with *Phytophthora*, pointing out that there is in fact no tangible basis of separation. She uses the binomial, *Phy. cambivora* (Petri) Buisman.

The genus *Pythiomorpha* Petersen (1910) founded on the single species *Pythiomorpha gonapodioides* Petersen (Fig. 73), is made the sole representative of a new family, Pythiomorphaceae, by Petersen. It is discussed at length by von Minden (1916), Buisman (1927), and Kanouse (1925). The vegetative mycelium occurs in plant substrata, twigs, fruits, etc., immersed in the water, and forms a prominent floating white mat. The hyphae are of small diameter and are provided with numerous small protuberances which give them a characteristically irregular appearance. Highly refractive granules, believed by Petersen to be cellulin, are present in the cytoplasm. The presence of these granules and the somewhat constricted aspect of the hyphae have led some workers to regard the species as intermediate between the Pythiaceae and Leptomitaceae. The extramatrical hyphae bearing the sporangia are cylindrical, straight, and unbranched. The sporangia are terminal, ovate, broader below and somewhat narrowed above, and have a definite papilla of dehiscence. They proliferate repeatedly, the sporangia which follow the primary being developed either within it or, by further growth of the hypha, at a considerable distance beyond its mouth. According to von Minden the swarmspores are delimited in a thin-walled vesicle at the apex of the sporangium. The formation of the vesicle is denied by Kanouse. The swarmspores are reniform

and laterally biciliate. After encystment the spore may emerge and undergo a second period of motility. Oogonia and oospores resembling those of *Phytophthora* are described by Kanouse. The oospore is sometimes developed parthenogenetically. Antheridia, when present, are paragynous. Although the irregular hyphae, proliferating sporangia, repeated swarmspore emergence, and saprophytic and aquatic habit are characters not outstanding in all species of *Phytophthora* they occur individually in various species of the genus. There seems to be no tangible basis for

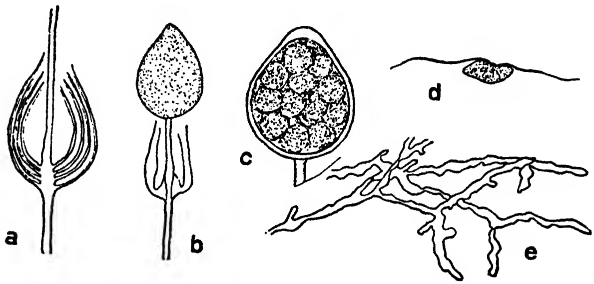

FIG. 73.—*Phytophthora gonapodioides* (Petersen) Buisman. (*a*) Nested aspect of sporangia resulting from proliferation. (*b*) Secondary sporangium formed beyond primary, the inner wall of the latter having been pulled upward. (*c*) Delimitation of swarmspores. (*d*) Swarmspore.' (*e*) Mycelium. (*After Kanouse 1925.*)

separation of the two genera. The species has been transferred to *Phytophthora* by Buisman. Recently Apinis (1930: 234) has transfered *Pythium undulatum* Petersen to *Pythiomorpha.*

The genus *Stigeosporium* West (1916; 1917) based on *S. marattiacearum* West, having a mycorrhizal relation with certain ferns, is as yet imperfectly understood. Though regarded by its author as related to *Phytophthora* it seems to be, in fact, wholly dissimilar. The peculiar thick-walled resting spores figured by West recall those of *Blastocladia* and *Allomyces.*

4. **Trachysphaera** Tabor & Bunting (1923)

This extremely interesting genus was recently founded on a single species, *T. fructigena* Tabor & Bunting (Fig. 74), cause of a disease of cocoa and coffee fruits in the Gold Coast Colony in Africa. The sexual stage is similar to that of the *infestans* group of *Phytophthora.* The antheridium forms a collar about the base of the oogonium, but the latter is ornamented with

prominent wart-like or sac-like protuberances which give it a striking appearance. The oospore is thin-walled. Its method of germination is unknown. The asexual stage as described is unlike that of any other member of the order. Hyphae form a subiculum beneath the epidermis of the host from which a dense mass of sporangiophores arises. The epidermis is ruptured and mealy masses of sporangia are formed on the surface of the host. The sporangiophore is variable in form. In its simplest type it is merely an erect hypha terminated by a single sporangium. The tip of the sporangiophore is usually enlarged, however, to form

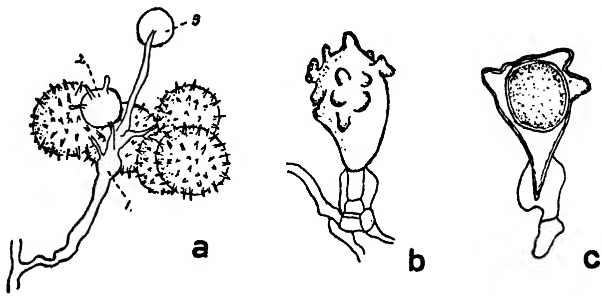

FIG. 74.—*Trachysphaera fructigena* Tabor & Bunting. (*a*) Sporangiophore with swollen vesicle (1) bearing a whorl of spherical echinulate sporangia and two other vesicles (2 and 3) which have not yet borne sporangia. (*b*) Rough-walled oogonium accompanied by an amphigynous antheridium. (*c*) Oogonium and oospore in longitudinal section. (*After Tabor and Bunting 1923.*)

a more or less globose vesicle from which a number of sterigmata arise, each terminated by a sporangium. Some of the sterigmata may grow farther and form other vesicles bearing additional sporangia. The sporangia ("conidia") are spherical, strikingly echinulate, and germinate by germ tubes.

The presence here of the amphigynous type of antheridium, hitherto known only in *Phytophthora*, gives the genus unusual interest. This is especially true in view of the fact that the asexual stage is unlike that of other members of the Oomycetes and recalls that of certain of the Mucorales. The proper position of the genus in the classification is perhaps in doubt.

Peronosporaceae

Mycelium intercellular in higher plants; haustoria developed and variously shaped in different genera; sporangiophores definite

in form, branched, arising from endophytic mycelium, protruding through the stomates, and bearing the sporangia in the air; sporangia deciduous, disseminated by the wind, germinating by swarmspores or germ tubes; sexual organs developed in the intercellular spaces; oogonia monosporic; oospore germinating by a germ tube.

The sporangiophores, protruding in great numbers from the stomates, form definite, whitish, grayish, or violet, mouldy patches on the surface of the host. The same thing occurs in some species of *Phytophthora* of the preceding family. The common name downy mildews was applied to these forms to distinguish them from the powdery mildews, an ascomycetous group (Erysiphaceae).

The sexual process in the family has been studied cytologically in several species representing the genera *Sclerospora*, *Plasmopara*, and *Peronospora*. In general, it does not differ strikingly from that described above for *Albugo candida*. A receptive papilla is formed, a coenocentrum is differentiated, and a true fertilization, terminated by a single nuclear fusion, occurs. A critical consideration of the details of the process in the various forms studied indicates a close relationship between the Albuginaceae and Peronosporaceae, and suggests the probability that the latter family is the more recently developed (Wager, 1900; Stevens, 1902; Rosenberg, 1903; Krüger, 1910).

Key to Genera of Peronosporaceae

I. Oospore wall confluent with that of the oogonium; sporangiophore typically stout with heavy branches clustered at its apex.
   1. **Sclerospora**, p. 212

II. Oospore wall not confluent with that of the oogonium; sporangiophore typically more slender.
   A. Sporangiophore consisting of a clavate or cylindrical trunk provided with a swollen apex from which short sterigma-like branches arise, each bearing a sporangium.
      2. **Basidiophora**, p. 214
   B. Sporangiophore provided with prominent branches.
      1. Branching monopodial to subdichotomous.
         a. Tips obtuse; branches arising more or less at right angles.
            3. **Plasmopara**, p. 215
         b. Tips more acute; branches forming more or less acute angles.
            4. **Peronoplasmopara**, p. 218

2. Branching dichotomous.
   a. Tips enlarged; sporangia apically papillate.
      (1) Tips disc-like, bordered by sterigmata bearing sporangia.
         5. **Bremia**, p. 219
      (2) Tips merely swollen.
         6. **Bremiella**, p. 220
   b. Tips acute; sporangia not papillate.
      7. **Peronospora**, p. 221

1. **Sclerospora** Schröter (1886: 236).

Mycelium intercellular, bearing small, usually knob-like, unbranched haustoria; sporangiophores typically stout (Fig. 75), composed of a main trunk and a compact group of rather short apical branches which are once to several times divided; branching dichotomous to indefinite; germination of sporangia by one or more germ tubes or by swarmspores; oospores unlike those of other genera of the family in that the exospore is confluent with the wall of the oogonium; method of oospore germination undetermined (Weston and Weber, 1928: 957; Melhus, Van Haltern, and Bliss, 1928: 335).

The genus includes about twelve species. They are more commonly found in the Orient than elsewhere. Several species occur in the United States. The majority are parasitic on Gramineae.

The type species, *S. graminicola* (Sacc.) Schröter, is common in the United States on various species of foxtail grass (*Setaria* or *Chaetochloa*) and has been reported (Melhus, Van Haltern, and Bliss, 1928: 304) on *Zea mays* (maize), *Euchlaena mexicana* (teosinte), *Panicum miliaceum*, and *Saccharum officinarum*. In other parts of the world its host range is similar. The species is characterized by abundant development of oospores (estimated at three and one-half million in a medium sized leaf) and a poorly developed, evanescent sporangial stage. The sporangia are broadly ellipsoidal to globose and germinate by swarmspores. The sporangiophore is stouter than in some other species, the main branches being few and stout, and the terminal branches conical. In later stages of the disease the terminal portion of the host plant tends to take on a characteristic shredded aspect. This is due to the disintegration of the tissue between the vascular bundles and the consequent development of fibrous tangles of dry bundles from which the oospores are gradually scattered. The inflorescence is often transformed by the development of elongate, leaf-like bracts which replace the usual floral parts.

The whole head may be sterile and abnormally green, *i.e.*, virescent. (Stevens, 1902; Butler, 1907; Kulkarni, 1913; Wilson, 1907 *b*; Weston and Weber, 1928; Melhus, Van Haltern, and Bliss, 1928, Weston, 1929 *a*, *b*, *c*.)

In 1921 *S. macrospora* Sacc. long known in Europe, was found on wheat in Kentucky and Tennessee (Weston, 1921 *b*). It has been reported also on *Bromus commutatus* in America and on various hosts abroad. Its life history is poorly understood.

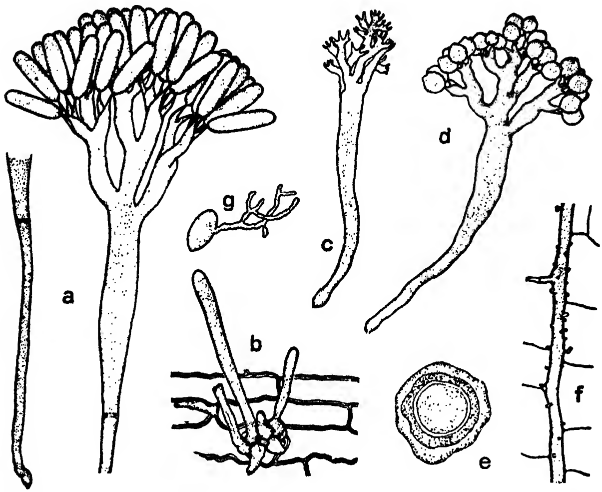

FIG. 75.—(*a*) *Sclerospora spontanea* Weston. (*b*-*e*) *S. graminicola* (Sacc.) Schröt. (*f*-*g*) *S. philippinensis* Weston. (*a*) Sporangiophore. (*b*) Sporangiophores emerging from stomate. (*c*) Young sporangiophore. (*d*) Sporangiophore bearing sporangia. (*e*) Oogonium containing oospore. (*f*) Intercellular mycelium with haustoria. (*g*) Germinating sporangium. (*e*, *after A. Fischer; others after Weston.*)

Two species common in the Philippines on maize, *S. philippinensis* Weston and *S. spontanea* Weston, have been studied critically by Weston (1920; 1921 *a*; 1923 *a*, *b*). In these forms the sporangiophore is more slender than in *S. graminicola* and the sporangia much more elongated. The species are characterized by abundance of sporangia and absence of oospores, the reverse of the situation in *S. graminicola*. The sporangia germinate, moreover, by germ tubes instead of by swarmspores as in that species. In this they resemble several other Oriental

species (Butler, 1913 *b*) also found on maize. The relation of sporangial production to environmental conditions is interesting. Sporangiophores develop only at night and protrude through the stomates while the surface of the host is covered with dew. Dispersal of sporangia also occurs at night, and seems to be accomplished by forcible ejection from the sterigmata.

A chart listing the known species of the genus and indicating geographical distribution, host range, and other data is given by Melhus, Van Haltern, and Bliss (1928: 304).

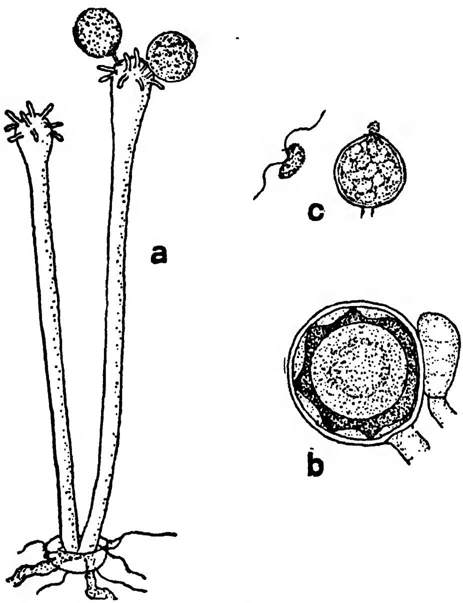

FIG. 76.—*Basidiophora entospora* Roze & Cornu. (*a*) Sporangiophores arising from stomate. (*b*) Oogonium with mature oospore. (*c*) Sporangium liberating swarmspores. (*After Cornu 1869.*)

2. **Basidiophora** Roze & Cornu [*Ann. Sci. Nat.* (ser. 5), **11**: 84, 1869].

Mycelium intercellular; haustoria small and knob-like; sporangiophore consisting of a cylindrical unbranched stalk terminating in a clavate enlargement over the surface of which short,

cylindrical, delicate sterigmata protrude bearing sporangia (Fig. 76).

The sporangium is almost globose, possesses a definite apical papilla, and germinates by swarmspores. Two species occur in North America, *B. entospora* Roze & Cornu on *Aster, Solidago, Erigeron,* and *Leptilon,* and *B. kellermanii* (Ellis & Halsted) Wilson on *Iva xanthifolia.*

3. **Plasmopara** Schröter (1886: 236).

Mycelium intercellular; haustoria unbranched and knob-like; sporangiophores (Fig. 78) protruding from the stomates, erect, solitary to densely fasciculate, monopodially branched, the branches arising more or less definitely at right angles to the main axis; secondary branches also at right angles; the terminal branches apically obtuse; sporangia small, hyaline, papillate, germination sometimes by germ tube, but in the majority of cases by swarmspores; oospores yellowish brown; the epispore wrinkled and sometimes somewhat reticulate; the oogonial wall persistent, but not fused with the epispore as in *Sclerospora* (Wartenweiler, 1917; 1918 *a, b*).

Oospore germination has been observed in but few species. Gregory (1912) pictures it for *P. viticola* (B. & C.) Berl. & De Toni (Fig. 77, *a, b*). In this species the oospore wall cracks open and a germ tube protrudes. At its end a sporangium similar to the summer sporangium is cut off, and germinates by swarmspores. A similar method of germination is to be expected in other species.

The genus is split by Wilson (1907 *b*) into two, *Rhysotheca* Wilson and *Plasmopara* (sensu strictu). The majority of the species are incorporated in *Rhysotheca.* One, *P. pygmaea* (Unger) Schröter, is retained in *Plasmopara.* In it, according to Wilson, swarmspores are not produced. Instead the sporangial wall ruptures, and the entire protoplasmic content escapes in a mass, forming a non-motile protoplast (perhaps enveloped in the endospore) which later germinates by a germ tube. Since the tips of the branches of the sporangiophore are obtuse, the branching not definitely dichotomous, and the sporangia hyaline, this peculiarity of germination is the only essential point in which this species differs from those assigned to *Rhysotheca.*

The genus *Pseudoplasmopara* Sawada (1922: 77) based on *Pseud. justiciae* Sawada on *Justicia procumbens* in Formosa is

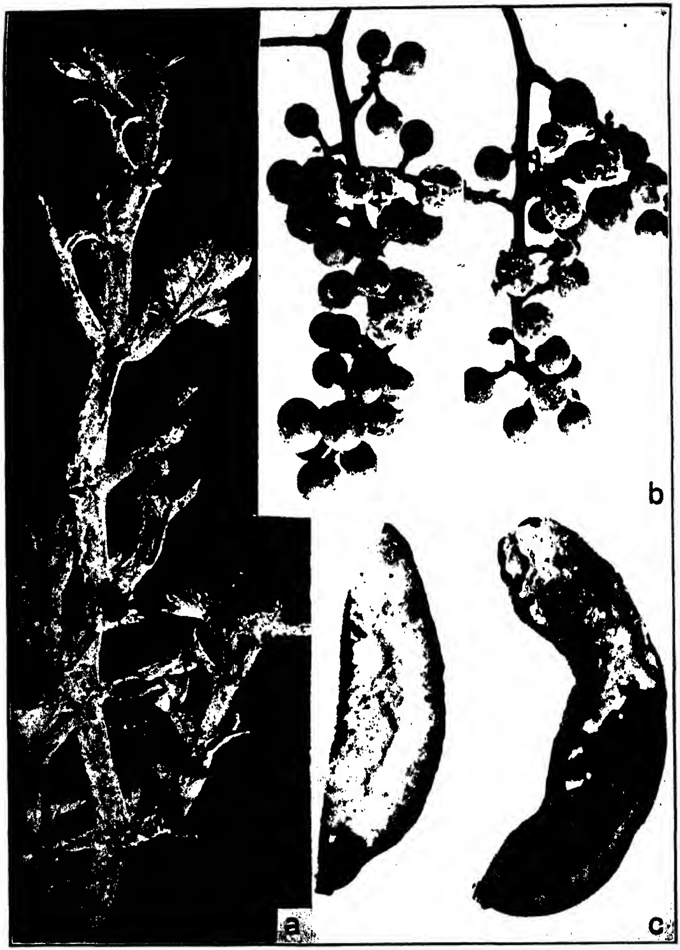

FIG. 77.—(*a*, *b*) *Plasmopara viticola* (Berk. & Curt.) Berl. & de Toni, on grape. (*c*) *Phytophthora phaseoli* Thaxter, on lima bean. (*Original.*)

described as having sporangia and sporangiophores like those of *Plasmopara* but with germination always by germ tube.

As the method of germination throughout the family is somewhat inconstant and to a degree dependent on the conditions of the environment it seems better to place the emphasis in generic separation on morphology rather than on differences in germination. On this basis the genera *Rhysotheca* and *Pseudoplasmopara* are here merged with *Plasmopara*.

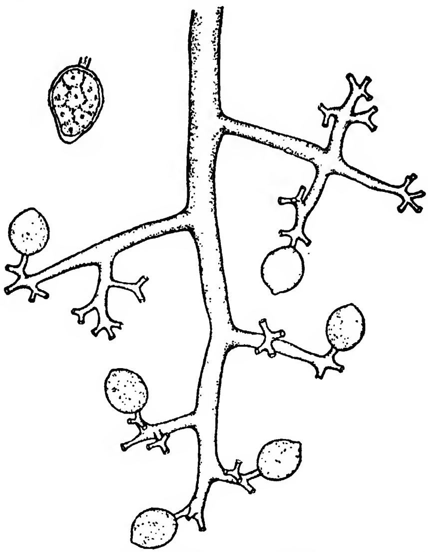

FIG. 78.—*Plasmopara australis* Swingle. Sporangiophore and sporangia. (*After Schwarze 1917.*)

Approximately fifteen species of Plasmopara are known for North America. Of these *P. viticola* (Berk. & Curtis) Berl. & De Toni., cause of downy mildew of cultivated and wild grapes, is best known. This species was first reported from the United States by Schwèinitz in 1834. It apparently originated in this country on the wild species of *Vitis*. It was well described by Farlow in 1876. Two years later it was discovered in the vineyards of southern France and very quickly became a menace to the grape industry. Its rapid spread over Europe and Asia

Minor, the strenuous efforts to stop its ravages, and the incidental and accidental discovery of bordeaux mixture are now well known to all students of plant pathology. The species also occurs on the Virginia creeper (*Psedera quinquefolia*) and related plants. Other well known species of the genus are:

Pl. geranii (Peck) Berl. & De Toni—on wild *Geranium*.

Pl. obducens Schröter—on *Impatiens*.

Pl. halstedii (Farlow) Berl. & De Toni—on *Ambrosia, Bidens, Erigeron, Eupatorium, Helianthus, Rudbeckia, Silphium*, and other members of the Carduaceae. This species has not been sufficiently studied taxonomically and perhaps should be subdivided into several. It has been studied cytologically by Nishimura (1926).

Pl. viburni Peck—on *Viburnum*.

Pl. ribicola Schröter—on *Ribes*.

Pl. pygmaea (Unger) Schröter—on various genera of the Ranunculaceae.

Pl. nivea (Unger) Schröter—on various genera of the Umbelliferae. It occurs on carrot and parsnip and has been reported in America from California.

4. **Peronoplasmopara** Berlese, in Clinton (1905 *a*: 329).
syn. *Pseudoperonospora* Rostowzew (1903: 422).

In the earlier investigations of the Peronosporaceae two species, *Peronospora cubensis* B. & C. and *Peronospora celtidis* Waite, were recognized as noteworthy in that their characters show them to be intermediate between *Peronospora* and *Plasmopara*. The first of these is the well known and common mildew of cucurbits. The other occurs on *Celtis occidentalis*. In the monographic treatment of the family by Berlese (1902: 123) both species are incorporated in the genus *Plasmopara*, a new subgenus, *Peronoplasmopara*, being established there for their reception. In these species, the sporangiophore branches in a subdichotomous manner, the branches arise at acute angles, and the terminal branchlets have subacute tips. The sporangia are large and tinted as in *Peronospora*, but have a prominent papilla and germinate chiefly by swarmspores as in *Plasmopara*.

The year following the erection of the subgenus *Peronoplasmopara* Berlese, the cucurbit organism *Peronospora cubensis* B. & C. was critically studied by Rostowzew. He published an extensive discussion of it, expressed the belief that it represents a distinct genus intermediate between *Peronospora* and *Plasmopara*, and applied to it the new name *Pseudoperonospora* (Rostowzew 1903: 422). Although he contrasted the species with those of *Peronospora* and *Plasmopara*, he failed to give a generic

diagnosis, and the reader is left in some doubt as to the essential characters of the genus. Article 38 of the International Rules of Botanical Nomenclature requires that a diagnosis accompany a new name in publication Since Rostowzew made no reference to the subgeneric diagnosis of Berlese he may be assumed to have been ignorant of its existence, and consequently article 49 of the Rules relating to the elevation of a subgenus to generic rank does not apply (see Curzi, 1926). In 1905 Clinton, realizing this situation and feeling that *Pseudoperonospora* would not stand, raised the subgeneric name *Peronoplasmopara* Berlese to generic rank and published a generic diagnosis. Clinton (1905 *a*: 334) discusses the situation at length, and the writer agrees with his conclusions. The name *Peronoplasmopara,* attributed by Clinton to Berlese, is, therefore, applied.

Since the erection of the genus on the two above named species, several others have been incorporated. These include *P. humuli* Miyake & Tak., the hop mildew, and *P. canabina* (Otth) Peglion, the mildew of hemp. A recently described species, *P. portoricensis* Lamkey (see Stevens, 1920) differs in that the sporangia are small and hyaline. It is not unlikely that the limits of the genus will be still further altered to include other species. Clinton has already pointed out that a critical study of all the species of *Plasmopara* and *Peronospora* may show that these genera grade into each other through so many forms that the attempt to recognize an intermediate genus such as *Peronoplasmopara* will only add to the difficulty of maintaining generic separations. Nevertheless, at present, recognition of the genus seems justified.

5. **Bremia** Regel (1843).

Mycelium intercellular, sending unbranched clavate to globose haustoria into the host cells; sporangiophores protruding from the stomates, where two or three have a common origin in a bulbous swelling of a single hypha; branching definitely dichotomous; each terminal branchlet broadened at its tip to form a shallow saucer-shaped disc from the edges of which several short sterigmata arise each bearing a sporangium; sporangium hyaline, with an apical papilla through which a germ tube is usually protruded.

Rarely germination is by swarmspores (Milbrath, 1923). The best known species *B. lactucae* Regel (Fig. 79) occurs on lettuce

and other Compositae. It is sometimes very destructive on cultivated lettuce, especially in the greenhouse. The literature on the genus is scanty. Recently several species have been described from the Orient by Sawada (1919) and Tanaka (1919).

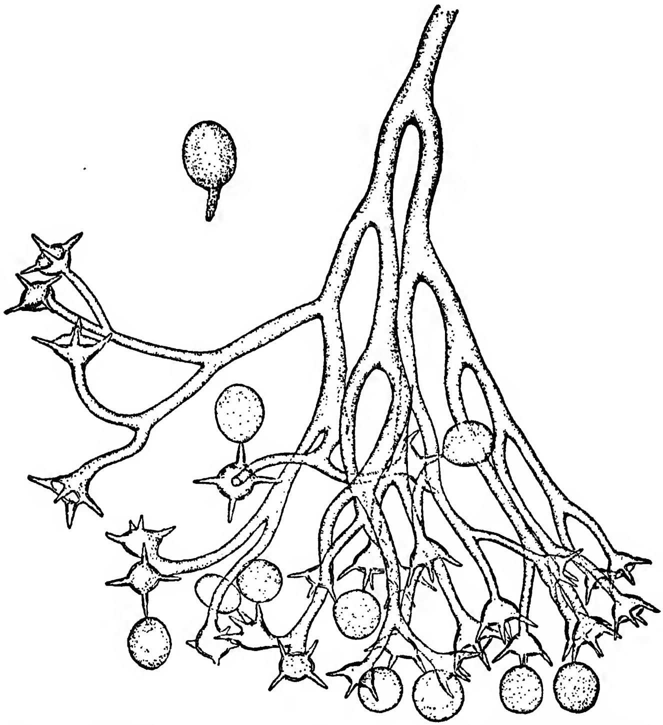

FIG. 79.—*Bremia lactucae* Reg. Sporangiophore and sporangia (*After Schwarze 1917.*)

6. **Bremiella** Wilson (1914 *b*: 195).

This is a monotypic genus based on *Plasmopara megasperma* Berlese (1903), occurring on violets. The branching of the sporangiophore is typically dichotomous, each ultimate branch being swollen at the apex to form an **apophysis** (Berlese, 1903: *fig. 16*). The sporangium is papillate and germinates by swarm-

spores. The genus may be regarded as intermediate between *Plasmopara* and *Bremia*, but the enlarged tips of the branches of the sporangiophore are not disc-like as in *Bremia*. Each bears but a single sporangium.

7. Peronospora Corda (1837: 20).

Mycelium intercellular; haustoria in a few species short and knob-like but in the majority filamentous and more or less branched; sporangiophore consisting of an erect trunk several (approx. 2–10) times dichotomously branched, the branches

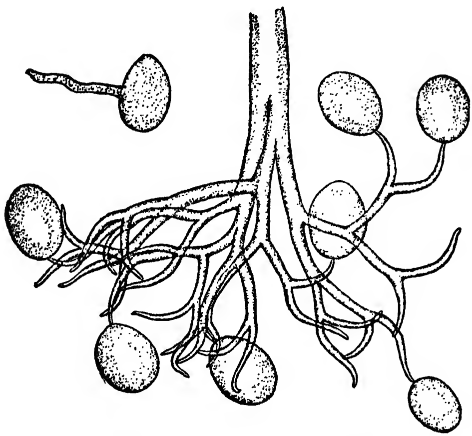

Fig. 80.—*Peronospora parasitica* (Pers.) de Bary. Sporangiophore and sporangia. (*After Schwarze 1917.*)

more or less reflexed and the terminal branchlets sharp pointed; the habit consequently more graceful than in *Plasmopara;* sporangia typically larger than in that genus, colored, lacking an apical papilla and germinating from an indeterminate point on the side by a germ tube; oospores more or less globose, smooth or variously marked, germinating by germ tubes.

Eriksson (1918 *b*: 19) states that in *P. spinaciae* Laubert [= *P. effusa* (Grev.) Tul.] the oospore is not a hibernating spore, but germinates *in situ* in the green leaf by several germ tubes which push out through the stomates and develop an aerial mycelium from which sporangia are cut off (Fig. 80). He says further that these sporangia germinate by swarmspores His

study, dealing chiefly with the **mycoplasm hypothesis,** is based largely on stained cytological preparations rather than on living material, and is not convincing. However, since swarmspore formation has been recently described in *Bremia* (Milbrath, 1923: 991) the demonstration of its occurrence in one or more species of *Peronospora* would not be wholly unexpected.

Peronospora is by far the largest genus of the order. Although Wilson has not yet monographed the species of North America he cites over forty of them in his host index (Wilson, 1908 *b*: 543). Gäumann (1923) in a monograph of the species of Switzerland lists one hundred and forty-two species of which nearly seventy are described as new. Following de Bary he subdivides the genus into four groups as follows:

I. Subgenus *Leiothecae* Schröter—Epispore of the oospore smooth or indefinitely wrinkled, never reticulate or verrucose.
  - *A*. Group *Parasiticae* de Bary—Oogonial wall thick, of two layers, not collapsing after the spore matures.
  - *B*. Group *Effusae* de Bary—Oogonial wall thin, collapsing after the spore matures.

II. Subgenus *Calothecae* de Bary—Epispore verrucose or covered with ridges which may or may not anastomose.
  - *A*. Group *Verrucosae* A. Fischer—Oospore with more or less hemispherical warts or with ridges which do not anastomose.
  - *B*. Group *Reticulatae* A. Fischer—Oospore with a regular network of anastomosing ridges.

The species in each group are separated primarily on the basis of host range, the species in each host family then being separated by differences in sporangial measurements. One old species, *P. parasitica* (Pers.) Fr. is broken up (Gäumann, 1917) into approximately twenty new species some of which are limited to a single host. The results of cross inoculation work correlated with minor differences in sporangial measurements provide the bases for separation. A number of other older species are similarly split. The paper contains an extensive bibliography and a wealth of information. The monographic treatises of Schröter (1889), Fischer (1892), and Berlese (1903), while older, are useful.

Two doubtful South American genera are included here for reference, *Chlorospora* Spegazzini (*Rev. Argentin. Hist. Nat.*, 1891: 29) and *Drepanconis* Schröter & Hennings (*Hedw.* 1896: 211). The first was based on *Ch. vastatrix* Speg. reported from onion bulbs, the second on *D. brasiliensis* Schröter & Henn. occurring on leaves and branches of *Nectandra*.

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CHAPTER IX

MUCORALES

Mycelium profusely developed, filamentous, richly **branched**, when young coenocytic, in age frequently provided with transverse septa, terrestrial, usually saprophytic, in some species parasitic, consisting of nutritive hyphae buried in the substratum and aerial hyphae on which the reproductive bodies are usually borne; the aerial mycelium usually prominent, the group having been designated in consequence the moulds; thick-walled, intercalary, globose to barrel-shaped **chlamydospores**, and thin-walled **oidia** not infrequently formed on the mycelium (Lendner 1908 *b*: *figs. 16–18*); sporangia borne on specialized sporangiophores, sometimes accompanied by or replaced by few-spored **sporangiola** or unicellular conidia; sexual reproduction accomplished by the conjugation of similar **gametangia (coenogametes)**, and resulting in the formation of a thick-walled **zygospore**; **azygospores** sometimes developed in the absence of the sexual fusion; zygospore germinating by a germ tube which usually bears a single large apical **germ sporangium**; swarmspores absent throughout the group.

In the lower members of the group asexual reproduction is accomplished by means of sporangiospores borne in large, globose to pyriform, many-spored sporangia. The septum which delimits the sporangium is often strongly convex, and appears as a more or less columnar protrusion of the sporangiophore into the sporangium. This apparent protrusion, termed the **columella**, usually remains in position after the sporangial wall has disintegrated, and the spores are sometimes found adhering to it.

The columella does not result in fact from a bulging upward into the sporangium of a transverse septum. It is formed in the position in which it lies at maturity, and is laid down along a prominent cleavage plane in the cytoplasm. Similar **cleavage planes** run progressively in all directions, arising from the columella, sporangial wall, and vacuoles, and finally cut the proto-

plasm into small usually uninucleate bits. These are then invested in walls and become the sporangiospores. This method of spore formation is typical of all sporangia, and contrasts with the phenomenon of **free cell formation** by which ascospores are formed in the Ascomycetes. The details of the two processes are given by Swingle (1903) and Harper (1899).

In the Mucorales as in the Peronosporales a gradual transition from the sporangium to the **conidium** is evident, endogenous spores being no longer developed in the higher forms. In intermediate conditions the sporangium exists as a deciduous, few-spored body to which the special name **sporangiolum** is applied. Although it is evident that the conidium is the homologue of the sporangium and has been derived from it in some cases at least directly through the sporangiolum, the application of the three terms to the three types of structure can be accomplished without appreciable ambiguity inasmuch as in this group few confusing border line conditions are encountered. The transition from sporangium to sporangiolum can be demonstrated (Thaxter 1914: 353) in *Blakeslea*, while in *Chaetocladium* and *Haplosporangium* the origin of the conidium from the monospored sporangiolum is evident.

In the majority of species the zygospore is formed as the result of the fusion of two gametangia essentially identical in size and shape. The conjugation process begins when two hyphae lying in contact are stimulated to develop a pair of lateral branches, **progametangia** (incorrectly termed progametes), at their point of contact. These branches, which are thus from the beginning adherent, swell, and a transverse septum forms in each. The terminal cell, thus delimited in each, functions as a **gametangium,** the remainder of the progametangium being termed the suspensor. The wall separating the two gametangia is then broken down and a fusion cell (**coenozygote**) results. The **zygospore** is usually formed in this cell, the wall of the cell finally forming the outer wall of the spore. In the Piptocephalidaceae the zygospore forms in a bud which develops from the fusion cell.

It has long been known that in some species of the Mucorales zygospores occur commonly in nature, while in others they are found infrequently if at all. Their production in the latter forms was assumed by earlier investigators to depend on some special condition of environment, and various methods of inducing their formation were followed, none of which could be relied

upon. Teachers of botany desiring to use the common bread mould in their laboratory work as illustrative of the Zygomycetes were often at a loss to obtain zygospores, and subcultures from zygospore producing material were in demand. Even these frequently failed to develop zygospores. The spontaneous appearance of zygospores on a variety of media and under widely different conditions was wholly unexplained.

The key to this mystery of zygospore production was discovered by Blakeslee, and the explanation, though entirely unexpected was very simple. Blakeslee (1904: 205) was working on the problem of zygospore formation in *Mucor mucedo* and obtained pure, zygospore producing cultures on agar. He found that cultures from single sporangia of this material never produced zygospores, but that if a mass of mycelium was transferred, zygospores appeared in abundance about the point of inoculation, decreasing in number as the growth widened. It was found also that mixed sporangial transfers from the center of the mass gave origin to zygospores, while similar transfers from the margin of the growth failed to do so. The culture which made clear the fundamental nature of zygospore production was prepared in the endeavor to discover whether the tendency to develop zygospores could be transmitted through the mycelium derived from the germination of a single sporangiospore. For this purpose dilution cultures were made from mixed sporangial transfers from the center of a zygospore group, one petri dish thus prepared containing only five spores. When the five mycelia which developed from these spores met, it was seen that an abundant growth of zygospores occurred along the line of apposition of certain of the mycelia, while between others none were formed. This culture showed, moreover, that a given mycelium would produce zygospores when meeting a second mycelium, and fail to do so on meeting a third, which would form them on meeting the second. Thus the culture indicated not only that two mycelia arising from different spores are necessary for the production of zygospores, but also that these spores are developed from the union of mycelia which are different in nature. Blakeslee confirmed these results by numerous observations on *Mucor mucedo*, and extended his investigation to other members of the order. He found that the majority of the Mucorales examined are of the type of *Mucor mucedo*, and he designates these as **heterothallic** forms, because two different thalli are necessary for zygospore formation. In

these forms any given thallus bears sporangiospores which give rise to thalli of the same nature as the parent thallus. He has cultivated the opposite strains of *Phycomyces nitens* and *Mucor mucedo* by means of sporangiospores for more than one hundred asexual generations without any apparent change in their sexual behavior. The two different strains of a heterothallic form can sometimes be distinguished by a slight difference in the luxuriance of their growth, although they are otherwise morphologically indistinguishable. On account of this distinction the terms plus (+) and minus (−) were suggested by Blakeslee for the two strains. Although he believed the difference to be a sexual one, he was unable to state which strain was male and which female.

In a few species of the Mucorales the zygospores were found to arise by the interaction of hyphae of a single mycelium derived from the germination of a single spore. Blakeslee termed such forms **homothallic.** To this group belong *Sporodinia grandis, Spinellus fusiger, Zygorhynchus spp., Dicranophora fulva, Absidia spinosa,* and a few species of *Mucor,* while the heterothallic group includes *Rhizopus nigricans, Mucor mucedo, Phycomyces nitens, Absidia caerulea* and a very considerable number of others.

Blakeslee made the further very interesting observation that **imperfect hybridization** (the production of the early stages of zygospores which never mature) will take place between opposite strains of different heterothallic species and between both (+) and (−) strains of heterothallic species on the one hand, and homothallic species on the other. A homothallic species placed between the two strains of a heterothallic species may, therefore, give rise to two lines of imperfect zygospores. This power of hybridization between different species of the Mucorales has made it possible to place in the proper category of (+) or (−) the strains of such heterothallic forms as *Mucor mucedo* in which there is no visible difference in the luxuriance of the two strains. It also makes possible the determination of the (+) or (−) character of the thalli in those heterothallic species in which only one strain has been obtained for study.

The results obtained by Blakeslee (1906 *a*) in the **germination of zygospores** have proved of particular interest. In the Mucorales the germ tube which arises from the zygospore usually bears a single sporangium termed the **germ sporangium,** though it may occasionally produce a branching mycelium. The examination of the spores in the germ sporangium with reference to their

(+) and (−) character is especially instructive. The conditions presented in the germ sporangium as determined for the three species, *Mucor mucedo*, *Sporodinia grandis*, and *Phycomyces nitens* represent three distinct types. The conditions are summarized by Blakeslee as follows:

1. The germination of the zygospores of the homothallic species, *Sporodinia grandis*, is pure homothallic, all the spores of the germ sporangium on germination developing homothallic mycelia.

2. The germination of the zygospores of the heterothallic species, *Mucor mucedo*, gives rise to germ sporangia in which all the spores are alike, either (+) or (−). Segregation of sex is accomplished at some point before the formation of the sporangiospores, and a single zygospore produces a germ sporangium containing spores of but one sort.

3. In the germination of the zygospores of the heterothallic species, *Phycomyces nitens*, segregation of sex occurs preceding the formation of the sporangiospores but is only partial. As a result the germ sporangium contains in addition to (+) and (−) spores, a few spores which on germination give rise to homothallic mycelia characterized by the production of contorted aerial outgrowths termed **pseudophores** and the occasional formation of homothallic zygospores. The sexual character in these homothallic mycelia is unstable and in their sporangia segregation again occurs and (+) and (−) spores and others which develop homothallic mycelia are produced. Finally the homothallic condition disappears. It is interesting to note that there is apparently no definite numerical ratio between the (+) and (−) spores formed in the germ sporangium, and it sometimes even happens that all the spores are of one sort.

If from analogy with other fungi segregation of sex may be assumed to occur in these moulds during the heterotypic mitosis, it is evident that this division does not occur at the same point in the life cycle of every species; nor does it occur in all of the diploid nuclei of a given species at the same time. This is evidenced by the presence of (+), (−), and "bisexual" spores in the same germ sporangium in *Phycomyces*. If a number of pairs of nuclei fuse in the mature zygospore of *Phycomyces* as described by Keene (1919) the presence of "bisexual" spores in the germ sporangium might be explained as due to the fact that certain of the nuclei retain their diploid character longer than others. This assumption has not as yet been substantiated by cytological observations.

Blackman (1906) objects to the use of the term sexual in connection with the fusion of the gametangia in the Mucorales. He states that the term sex as applied to organisms in general cannot be used where the fusing cells are morphologically

identical. For such cases he prefers the term **syngamy (syngametic).** Blakeslee (1906 *b*) feels that the similarity of the gametangia does not in the least detract from his conclusion that the differentiation into (+) and (−) strains is a sexual one. He points out that the use of the term **isogamy** (the conjugation of equal gametes in which no differentiation of sex can be distinguished) has only a morphological application among the Mucorales, since sexually the two gametangia which unite have diametrically opposite characters. The mutual indifference of two mycelia of the same sex and the active sexual reaction between mycelia of opposite sex which leads to the formation of zygospores when the mycelia are of the same species, indicate that the gametes are fundamentally different. In no species, however, either homothallic or heterothallic, in which the process of conjugation has been carefully followed, do the progametangia grow toward each other as has been commonly believed. They arise from the stimulus of actual contact between hyphae which touch each other, and are from the very beginning adherent.

In order to determine the sexual identity of the (+) and (−) strains, and to enable him to substitute the terms male and female, Blakeslee (1913; 1915) has performed some interesting experiments. In the heterothallic group no species has been discovered in which the gametangia differ constantly in morphology. The differences in size occasionally noted in *Rhizopus nigricans* and others are neither constant nor correlated with the (+) and (−) condition. In the homothallic group several well known species are **heterogametangic,** the gametangia differing strikingly in size and shape. To this category belong *Zygorhynchus moelleri*, *Zy. heterogamus*, *Absidia spinosa*, and *Dicranophora fulva*. Blakeslee feels that from analogy with the Oomycetes the larger gametangium may be considered female and the smaller male. Upon this basis if a sexual reaction could be established between these unequal gametangia and the (+) and (−) strains of a heterothallic species, the strain reacting with the larger female cell would be considered male, and that reacting with the smaller male cell would be considered female. Only a single heterogametangic species (*Absidia spinosa*) was found which would give reactions with both (+) and (−) strains, and only a single heterothallic species (*Mucor hiemalis*) which would react with both male and female gametangia of this heterogamic

homothallic species. The difficulties of technique encountered in following the sexual reactions in a tangle of filaments were overcome by growing the homothallic species in a petri dish between the (+) and (−) strains of the heterothallic species, and cutting channels in the agar between the different thalli. The reacting filaments could then be studied in mid-air in the channels. It was found that the sexual reaction occurs between the larger female gametangium and the (−) strain on the one hand, and between the smaller male gametangium and the (+) strain on the other. Therefore the conclusion is reached that the (+) strain of the heterothallic species is female and the (−) strain male. Subsequently, in his laboratory a study of the biochemical differences between strains has tended to substantiate this conclusion (Satina and Blakeslee, 1926 *a*, *b*; 1927).

A good resumé of the work on various aspects of sexuality in the group was given by Blakeslee (1920 *b*). In later years other investigators have somewhat broadened the field of our knowledge in the Mucorales, and Blakeslee's prediction that heterothallic forms would be discovered in other groups of the fungi has been fulfilled in the Saprolegniales, Peronosporales, and other groups both of the lower and higher fungi.

In several genera of the Mucorales species exists which are parasitic on other members of the order. Burgeff (1924) has studied several of these forms critically and advances the interesting hypothesis that they have become parasitic as a result of attempts at hybridization. He found that in the case of *Mucor* (*Parasitella*) *simplex* the (+) strain parasitizes only the (−) strain of the host *Absidia glauca*, while the (−) strain parasitizes only the (+) strain. In other cases the experimental results are less conclusive, and Satina and Blakeslee (1926 *b*) question the possibility of a wide application of the theory.

The nuclear phenomena which accompany conjugation of the gametangia and maturation of the zygospore are as yet imperfectly understood. The small size of the nuclei and the presence of a large amount of oil in the zygospore render the problem of staining a difficult one. A considerable number of forms have been investigated, but the published accounts are contradictory, incomplete, and unconvincing. All students of the group have agreed that the progametangia and young gametangia are multinucleate, and several describe the disintegration

of supernumerary nuclei. Dangeard (1906 *a*, *b*), Moreau (1911 *a*, *b*, *c*; 1912 *a*, *b*; 1913 *a*, *b*), and Keene (1914; 1919) describe nuclear fusions in the young zygospore between many pairs of nuclei, while Lendner (1908 *a*) and McCormick (1912) find evidence indicating that only a single nuclear fusion occurs. Dangeard and McCormick describe cytoplasmic bodies comparable to the **coenocentrum** of the Peronosporales, and the latter author states that the two nuclei present in the mature zygospore lie embedded in the coenocentrum. Keene, on the other hand, regards these bodies as undoubtedly related to the **elaioplasts** found in many other plants, which have for their function the elaboration of oil for reserve food. They occur in considerable numbers in the young zygospore, progressive fusions resulting ultimately in the formation of one or two large bodies saturated with oil. The mature zygospore is often practically filled with oil, the cytoplasm and nuclei being confined to a thin parietal layer next to the wall. Following nuclear fusion it is assumed that reduction division occurs in the zygospore before germination, but the facts have not been determined. Perhaps, as described for *Albugo*, some species characterized by a single nuclear fusion and others by a multiple fusion occur in this group. It is particularly unfortunate that the extremely interesting and suggestive experimental data of Blakeslee cannot now be explained from cytological data.

The order, Mucorales, as here constituted contains seven families, approximately thirty genera, and about four hundred described species. The most satisfactory general taxonomic treatments of the group are those of Fischer (1893) and Lendner (1908 *b*).

Key to Families of Mucorales

1. Sporangium when present globose to pyriform, many-spored, in some genera accompanied by, in others replaced by, few-spored sporangiola or unicellular conidia; zygospore formed in the fusion cell which results from the copulation of the gametangia.
   A. Sporangium when present containing a columella; zygospore not enveloped by a layer of interwoven hyphae.
      1. Sporangium always formed; sporangiola and conidia lacking.
         a. Sporangial wall thin, not cutinized.
            1. **Mucoraceae**, p. 242
         b. Sporangial wall heavily cutinized in the upper portion.
            2. **Pilobolaceae**, p. 251

2. Sporangium either accompanied by or replaced by sporangiola or conidia.
   a. Sporangium present, accompanied by sporangiola, both usually formed on the same sporangiophore.
   3. **Thamnidiaceae**, p. 253
   b. Sporangia often absent; when present solitary, not borne on the same sporangiophore with sporangiola or conidia.
      (1) Sporangium absent; conidia covering sub-terminal enlargements of branches of the conidiophore.
      4. **Chaetocladiaceae**, p. 257
      (2) Sporangium present in some genera, absent in others; sporangiola or conidia present in all cases, and covering terminal capitate enlargements of the branches of the sporangiophore or conidiophore.
      5. **Choanephoraceae**, p. 258

B. Sporangium when present lacking a columella; zygospore where known enveloped by a thick layer of interwoven hyphae; sporangiola and conidia formed in some cases, when present isolated, not covering an enlargement on the sporangiophore or conidiophore.
6. **Mortierellaceae**, p. 264

II. Sporangium narrowly cylindrical or rod-like, relatively few-spored; sporangiospores arranged in a single row, at maturity having the aspect of a chain of conidia due to the dissolution of the sporangial wall; zygospore usually formed in a bud put out by the fusion cell which results from the copulation of the gametangia.
7. **Piptocephalidaceae**, p. 270

Mucoraceae

Large, globose to pyriform, multispored sporangia formed in all genera, not shot away; sporangiola and conidia lacking; sporangial wall thin, not cutinized; zygospore not enclosed in a definite hyphal envelope.

Key to Genera of Mucoraceae

I. Sporangiophore indeterminate, elongating indefinitely, branching in a cymose manner, not bearing a terminal sporangium; branches circinate; sporangial wall persistent.
   A. Sporangium pyriform; columella hourglass shaped.
   1. **Pirella**, p. 243
   B. Sporangium globose; columella cylindrical to conical.
   2. **Circinella**, p. 244

II. Sporangiophore determinate, simple or branched, terminal sporangium always formed; branches only rarely circinate; sporangial wall evanescent.

A. Sporangiophores arising from aerial, arching stolons which develop rhizoids at points of contact with the substratum.

1. Sporangiophores borne on the arching internodes of the stolons between the rhizoid-bearing nodes; sporangia pyriform.

a. Suspensors of the zygospore provided with prominent circinate outgrowths.

3. **Absidia**, p. 244

b. Suspensors lacking outgrowths.

4. **Mycocladus**, p. 245

2. Sporangiophores arising in a fascicle from the node of the stolon opposite the tuft of rhizoids; sporangia globose.

5. **Rhizopus**, p. 245

B. Sporangiophores arising directly from the mycelium.

1. Aerial mycelium ornamented with short, lateral, thorn-like branches.

6. **Spinellus**, p. 246

2. Aerial mycelium lacking such thorn-like branches.

a. Sporangiophore branching repeatedly at the apex in a dichotomous fashion; zygospores borne on similarly branched aerial zygophores.

7. **Sporodinia**, p. 247

b. Sporangiophore unbranched, or branching in a monopodial or sympodial manner; zygospores borne on the mycelium.

(1) Sporangiophore unbranched, stiffly erect, with metallic iridescence; suspensors of zygospore provided with rigid dichotomously branched outgrowths.

8. **Phycomyces**, p. 248

(2) Suspensors lacking definite outgrowths.

(*a*) Gametangia strikingly dissimilar.

9. **Zygorhynchus**, p. 249

(*b*) Gametangia essentially alike.

10. **Mucor**, p. 250

1. **Pirella** Bainier (1883: 84).

Sporangiophore elongating indefinitely, not bearing a terminal sporangium, branching in a cymose manner; the branches circinate, terminated by pyriform sporangia; sporangial wall persistent, incrusted with crystals of calcium oxalate; columella very large, shaped like an elongate hourglass; zygospores unknown.

The genus is imperfectly known, containing only the type species, *P. circinans* Bainier. It corresponds with *Circinella*

except in the shape of the sporangium and columella, and may represent merely an atypical member of that genus.

2. **Circinella** van Tieghem & le Monnier (1873: 298).

Sporangiophore elongating indefinitely, not bearing a terminal sporangium, branching in a cymose manner; the branches circinate, single or in groups, terminated by globose sporangia; sporangial wall persistent, incrusted with crystals of calcium oxalate, finally rupturing in such a manner as to leave a prominent collar at the base around the columella; columella large, cylindrical to conical.

Lendner (1908 *b*: 101) includes seven species in the genus, and others have been described since (*Saccardo Syll. Fung.*, **24**: 1926). In *C. umbellata* zygospores are described by Bainier (1903: 170).

3. **Absidia** van Tieghem (1876: 350).

Mycelium forming repeatedly branched, arching stolons, rooted at points of contact with the substratum; sporangiophores

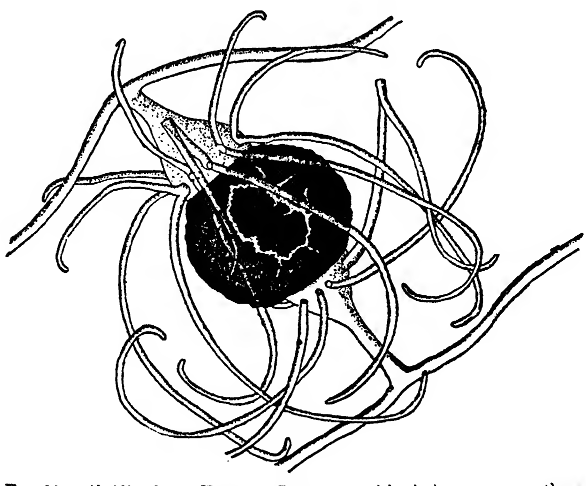

FIG. 81.—*Absidia glauca* Hagem. Zygospore with circinate outgrowths arising from the suspensors. (*After Lendner 1908.*)

erect, straight, usually in fascicles, more rarely single, arising from the elevated arching internodes of the stolons, not opposite the rhizoids; sporangia terminal, pyriform; sporangial wall

neither incrusted nor thickened, thin, soon disintegrating; columella conical to hemispherical, with a papillate apical prolongation which is sometimes drawn out into a rather long spine; sporangiospores small; zygospores borne on the stolons; one or both suspensors provided with prominent circinate outgrowths which tend to envelope the zygospore (Fig. 81).

The genus contains about twenty species. In its sporangial characters it corresponds with *Mycocladus*, and in its possession of stolons recalls *Rhizopus*. The genera *Tieghemella* Berlese & de Toni (*Saccardo Syll. Fung.*, **7**: 215, 1888), *Proabsidia* Vuillemin (1903 *b*: 119), *Pseudoabsidia* Bainier (1903: 153), and *Lichtheimia* Vuillemin (1903 *b*: 119) are here, as in Lendner (1908 *b*: 129), merged with *Absidia.*

4. **Mycocladus** Beauverie (*Ann. Univ. Lyon*, **3**: 1900).

Corresponding with *Absidia* in mycelial and sporangial characters, but differing in that the suspensors of the zygospore lack circinate outgrowths.

The genus contains only the type species, *M. verticellatus* Beauv., but species tentatively included in *Absidia*, in which zygospores are as yet unknown, may later be found to belong here. The genus is merged with *Absidia* by Lendner (1908 *b*: 129).

5. **Rhizopus** Ehrenb. (*Nova Acta Acad. Leopold.*, **10**: 198, 1820).

Aerial arching stolons developed from the nutritive mycelium as in *Absidia*, at points of contact with the substratum forming a tuft of repeatedly branched rhizoids (Fig. 82); sporangiophores arising from the stolon exactly opposite the point of origin of the rhizoids, usually unbranched and fasciculate; sporangia terminal, large, globose, many-spored; columella prominent, more or less hemispherical; sporangial wall not cutinized, at maturity almost wholly disappearing; sporangiospores globose to oval or angular, smooth or marked by longitudinal striations, rarely echinulate; zygospores formed from the nutritive mycelium or from the stolons; suspensors lacking outgrowths (Fig. 83).

A rather large genus containing approximately thirty species the best known of which is *R. nigricans* Ehrenberg, type of the genus. In the papers of Pound (1894: 98), Wilson (1906: 560), Sumstine (1910: 129), and Povah (1917: 248) the nomenclatorial problem presented by this species is discussed. In the treatment of Sumstine it is made the type of the genus *Mucor*, the name

Rhizopus disappears entirely, and *Hydrophora* Tode includes the species usually placed in *Mucor*.

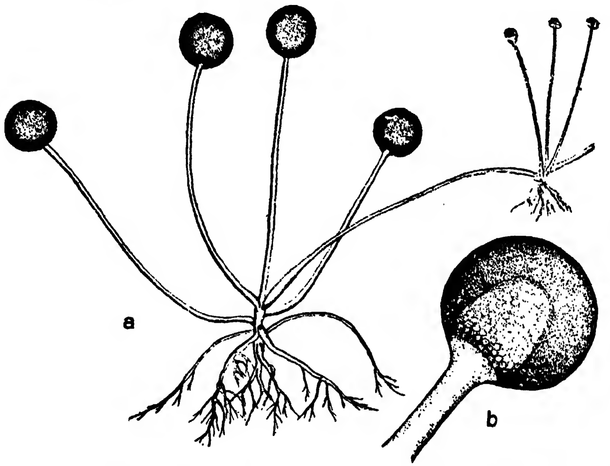

FIG. 82.—*Rhizopus nigricans* Ehrenberg. (*a*) Fascicle of sporangiophores arising opposite the rhizoids, and connected by a stolon with another group. (*b*) Sporangium enlarged to show columella and spores. (*After Atkinson 1908.*)

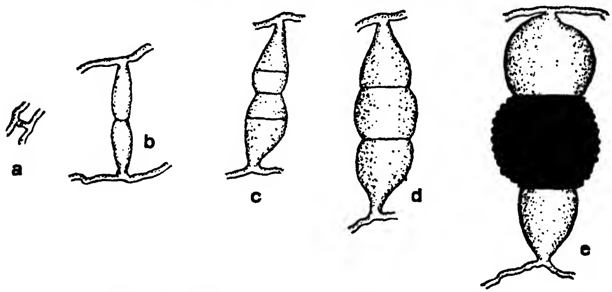

FIG. 83.—*Rhizopus nigricans* Ehrenberg. (*a*) Adjacent hyphae united by young progametangia. (*b*) Progametangia. (*c*) Gametangia and suspensors. (*d*) After fusion of gametangia. (*e*) Mature zygospore. (*Original.*)

For a taxonomic separation of species consult Lendner (1908) and Hanzawa (1914: 230).

6. **Spinellus** van Tieghem (1875: 66).

Vegetative mycelium buried in the substratum, consisting of delicate, hyaline hyphae; aerial mycelium well developed, brown,

profusely branched, ornamented with short, lateral, thorn-like branches; sporangiophore erect, unbranched, usually tapering to a swollen base, bearing a single, terminal, globose sporangium; sporangial wall delicate, hyaline, not incrusted; columella rounded to nearly cylindrical; zygospores borne only on the thorny mycelium; suspensors not thorny, having the appearance of tongs, not twining, developing the zygospore between their ends.

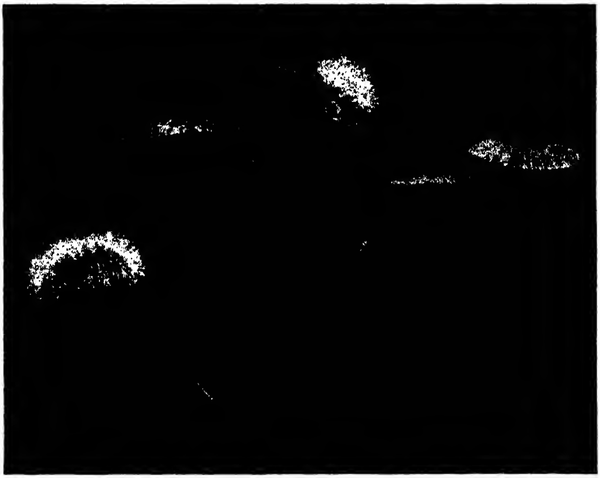

Fig. 84.—*Spinellus macrocarpus* Corda on *Mycena praelonga* Peck. (*Original.*)

A small genus of four or five species, parasitic on Agaricaceae and other higher fungi (Fig. 84). It is incorporated in *Mucor* by Schröter (1893: 125), but is given generic rank by Fischer (1892: 220) and Lendner (1908 *b*: 51).

7. **Sporodinia** Link, in Linnaeus Species Plantarum (4 edit.) **6**: 94, 1824; also see Tulasne (*Compt. Rend. Acad. Paris* **15**: 617, 1855).
syn. *Syzygites* Ehrenberg (*Sylvae Myc. Berol.*, p. 25, 1818).

Mycelium not forming stolons, profusely developed, occasionally septate; sporangiophores erect, abundantly septate, branching at the apex repeatedly in a dichotomous fashion: each branch

terminated by a more or less globose sporangium; sporangial wall neither cutinized nor incrusted, very thin and soon disintegrating; columella large, hemispherical; sporangiospores spherical, smooth, dark brown; zygospores developed on specialized erect, dichotomously branched, aerial hyphae, termed **zygophores;** copulating branches lateral on the zygophore; the zygospore formed between their tips as in *Mucor;* species homothallic (Fig. 85).

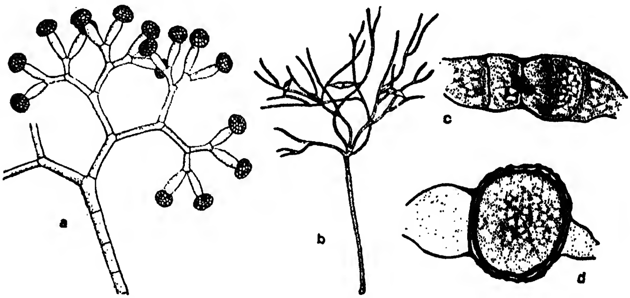

FIG. 85.—*Sporodinia grandis* Link. (*a*) Sporangiophore and sporangia. (*b*) Zygophore showing conjugating gametangia. (*c*) Gametangia and suspensors. (*d*) Mature zygospore. (*a, after Lendner 1908; b, after de Bary 1864; c, d, after Keene 1914.*)

Link based his description of *Sporodinia* on the sporangial stage alone. The zygophore and zygospore were described earlier by Ehrenberg who founded the genus *Syzygites* on them. Tulasne emended the generic description of *Sporodinia* to include both stages, and Brefeld later, by germinating the zygospores, proved that the two stages do in fact arise from the same mycelium.

The species *S. grandis* Link, type of the genus, is apparently the only known species, it having been included in the genus under a considerable number of specific names by various students.

8. **Phycomyces** Kunze and Schmidt (*Mycol. Hefte*, **2**: 113, 1823).

Mycelium wide-spreading in and on the substratum, richly branched; stolons absent; sporangiophores simple, stiffly erect, possessing a pronounced metallic iridescence, often exceptionally tall, reaching a length in some cases of ten or twelve inches, though usually shorter; sporangia terminal, large, globose, with a pyriform apically broadened columella; sporangial wall not

cutinized, somewhat incrusted with crystals of calcium oxalate, soon disintegrating; sporangiospores smooth, yellowish, ellipsoidal; zygospores formed on the mycelium; copulating branches shaped like tongs and forming the zygospore between their tips; suspensors provided with dichotomously branched, dark brown, rigid outgrowths, which radiate in various directions and have the aspect of antlers (Fig. 86), not enclosing the zygospore as in *Absidia*.

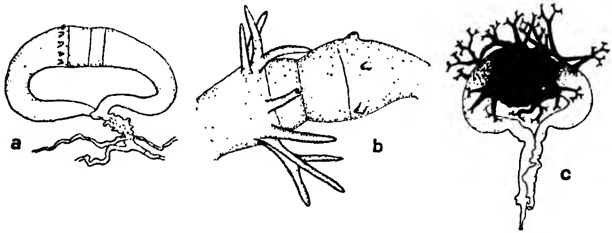

FIG. 86.—*Phycomyces nitens* (Agardh) Kunze. (*a*) Early stage in conjugation showing outgrowths arising from one of the suspensors. (*b*) Same somewhat later. (*c*) Mature zygospore; the outgrowths from the suspensors rigid and dichotomously branched. (*a, after Blakeslee, 1904; b, after Keene 1919;* c, *after van Tieghem and le Monnier 1873.*)

The best known species is *P. nitens* (Agardh) Kunze & Schmidt. At least five other species have been recognized: *P. splendens* Fries, *P. microsporus* van Tieghem, *P. pirottianus* Morini, *P. spinulosus* Morini, and *P. blakesleeanus* Burgeff.

9. **Zygorhynchus** Vuillemin (1903 *a*: 116).

Sporangial stage as in *Mucor;* zygospore formed in a characteristic manner from wholly dissimilar gametangia (Fig. 87); all species homothallic; genus merged with *Mucor* by Lendner (1908 *b*:72).

The genus contains relatively few species: *Z. heterogamus* Vuillemin (1903 *a*: 117); *Z. moelleri* Vuillemin (1903 *a*: 117), *Z. vuilleminii* Namyslowski (1910 *b*: 152), *Z. dangeardi* Moreau (1912 *a*: 67), *Z. bernaldi* Moreau (1913 *c*: 256), *Z. japonicus* Kominami (1914: 3).

The details of zygospore formation are discussed by Gruber (1912: 126), Atkinson (1912: 151), and Blakeslee (1913: 241). The terminal portion of an erect hypha is delimited by a septum from the part below. A lateral branch then pushes out just beneath the septum, grows upward, and recurves to meet the side

of the main hypha above the septum. At the point of contact the main hypha pushes out and cuts off a small gametangium. The much enlarged tip of the lateral branch cuts off the other. The zygospore formed by their union is thus always homothallic in origin. The termination of the main hypha is often turned to one side, and projecting beyond the zygospore as a slender prolongation gives the zygophoric apparatus a characteristic aspect.

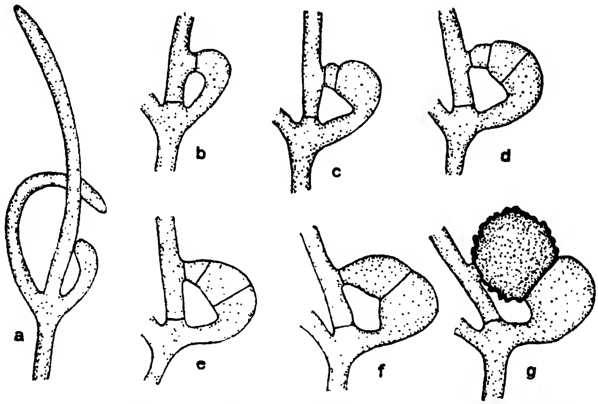

FIG. 87.—*Zygorhynchus heterogamus* Vuillemin. (*a–g*) Successive stages in conjugation terminating in formation of zygospore. (*After Blakeslee 1913.*)

10. **Mucor** Micheli, in *Nova Plantarum Genera*, p. 215, *pl. 95*, 1729; also see Link in Linnaeus *Species Plantcrum* (4 edit.), **6**: 80, 1824.

syn. *Hydrophora* Tode (*Fung. Meckl.*, **2**: 5, 1791).

Mycelium developed profusely both in and on the substratum, lacking definite rhizoids and stolons; sporangiophores not fasciculate as in *Rhizopus*, arising singly from the mycelium, erect, simple or somewhat branched in a monopodial or sympodial manner; all the branches terminated by sporangia; sporangia large, globose, many-spored; sporangial wall evanescent in most species, not cutinized, more or less incrusted with crystals of calcium oxalate; columella always present, various in shape; sporangiospores globose to ellipsoidal, with a thin, smooth wall; zygospores borne on the mycelium; suspensors lacking outgrowths; copulating branches lying end to end, forming a straight

line, not having the tongs-like aspect seen in certain other genera; terminal or intercalary, smooth, hyaline chlamydospores found in some species.

The genus is the largest in the Mucorales, over one hundred and fifty species being described by Saccardo (Sylloge Fungorum) for the world, and over fifty by Lendner (1908 *b*) for Switzerland. The genus is a difficult one for the taxonomist. Notes of interest on American species are given by Povah (1917).

The genera *Parasitella* Bainier (1903: 153), *Chlamydomucor* Brefeld (1889: 223; also see *Calyptromyces* Karst. in Sumstine 1910: 145), and *Glomerula* Bainier (1903: 154) are here embraced in *Mucor* (see Lendner 1908 *b*: 69, 71, 77).

Pilobolaceae

Sporangium discoid to lenticular, multispored, in most species provided with a prominent sub-sporangial vesicle and at maturity shot away; lower portion of sporangial wall thin and light-colored; upper part heavily cutinized and black; sporangiola and conidia lacking; zygospore not enclosed in a definite hyphal envelope, formed at the point of union of conjugating branches which have the aspect of closed tongs.

Key to Genera of Pilobolaceae

I. Sporangiophore provided with a large subsporangial vesicle; sporangium, accompanied by columella, forcibly discharged from the sporangiophore at maturity.

1. **Pilobolus, p. 251**

II. Sporangiophore lacking a subsporangial vesicle; sporangium not shot away.

2. **Pilaira, p. 253**

1. **Pilobolus** Tode (*Schrift. Naturf. Freunde Berlin*, **5**: 46, 1784).
syn. *Hydrogera* Web. & Wigg. (*Prim. Fl. Holstat.*, p. 110, 1780); see Sumstine (1910: 136).

Sporangiophore erect, unbranched, apically enlarged to form a prominent, clavate, subsporangial vesicle (Fig. 88), frequently also swollen at its point of origin from the mycelium, usually separated from the mycelium by a septum and anchored to the substratum by rhizoids; sporangium solitary, apical, discoid to lenticular, many-spored; provided with a central columella of much smaller diameter than the subsporangial swelling, the upper half of the membrane thickened and black, the lower half thin

and light colored; the mature sporangium discharged with violence from the end of the sporangiophore, commonly projected for several feet, the columella being carried away with it; zygospore formed at the point of union of conjugating branches which lie in such a position as to give the appearance of a pair of tongs.

The genus contains a dozen or more species. It is particularly interesting on account of the phenomenon of sporangial discharge which anticipates conditions in the following order, where such a discharge commonly occurs. An entertaining discussion of the mechanism which accomplishes discharge is given by Buller

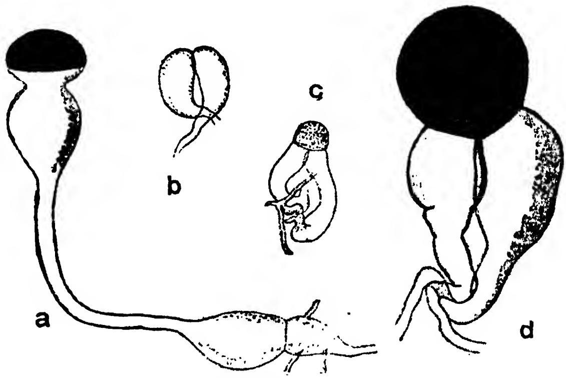

Fig. 88.—*Pilobolus crystallinus* (Wiggers) Tode. (*a*) Sporangiophore, subsporangial vesicle and sporangium. (*b–d*) Stages in zygospore formation. (*After Zopf 1888.*)

(1921). He finds that the neck of the subsporangial vesicle ruptures just beneath the sporangium, and that sudden contraction of the sporangiophore results in the squirting out of a jet of cell sap on which the sporangium is carried through the air. His experiments have demonstrated also that the vesicle functions as an **ocellus** (simple eye), and directs the tip of the sporangiophore toward the light in order that the sporangium may be discharged out of the crevices of the substratum into the lighted open. These fungi are found in nature on dung of herbivorous animals, and the spores germinate only after passing through the alimentary canal. The surface of the sporangial wall is adhesive. The sporangium falling on the grass or other herbage, adheres, is later eaten by the browsing animal, and enabled to complete its life

cycle. It is essential, therefore, that the sporangium be discharged toward the light rather than into the crevices of the substratum. The subsporangial vesicle functions as a lens in much the same way as does a flask filled with water. If the rays of the sun strike on one side of the vesicle they are refracted through it and converge on the opposite side forming a spot of light. The protoplasm at that point receiving thus a heliotropic stimulus, growth and elongation occur on that side of the sporangiophore. In consequence the sporangium is turned toward the light until the rays strike it head on. A condition of physiological equilibrium is then reached and the turning movement ends.

2. **Pilaira** van Tieghem (1875: 51).

Sporangiophore erect, unbranched, lacking a subsporangial vesicle; sporangium terminal, not shot away, when young globose; the membrane in the upper hemisphere black and thickened as in *Pilobolus*, below thin, hyaline, at maturity greatly distended, and finally disappearing; columella flat to globose, not falling away; zygospore formed as in *Pilobolus*, the conjugating branches erect and tending to twine about each other.

At least four species, all of them from dung, have been described in this genus. The possibility that they were based on abnormal material of *Pilobolus*, leads the writer to regard the genus as somewhat doubtful.

Thamnidiaceae

Sporangia and sporangiola formed together, usually on the same sporangiophore; sporangium large, multispored, thin-walled, and provided with a columella; sporangiolum much smaller, lacking a columella, provided with a thicker persistent wall, and falling away at maturity; zygospore not enclosed in a hyphal envelope.

Key to Genera of Thamnidiaceae

I. Spores in the sporangium differing in size and shape from those in the sporangiola; sporangiolum clasped at the base by several sharp-pointed claw-like branches.

1. **Dicranophora,** p. 254

II. Spores in sporangium like those in sporangiola; branch bearing sporangiolum lacking terminal claw-like projections.

2. **Thamnidium,** p. 255

1. **Dicranophora** Schröter (*Jahresb. Schles. Gesell. Vaterl. Cultur*, **64**: 184, 1886).

Mycelium imbedded in or creeping over the substratum, giving rise to erect, sparingly septate sporangiophores bearing sporangia and sporangiola (Fig. 89); sporangiophore simple or branched, when simple terminated by a single large many-spored sporangium; several such sporangia sometimes formed on a single sporangiophore as the result of cymose branching; sporangiophores usually provided with lateral branches, which divide repeatedly

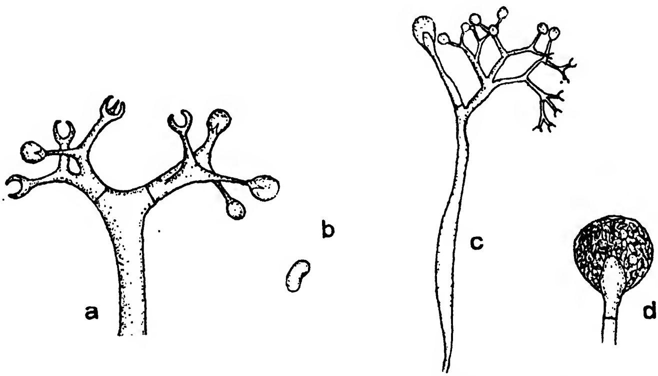

FIG. 89.—*Dicranophora fulva* Schröter. (*a*) Sporangiola. (*b*) Spore from sporangiolum. (*c*) Sporangiophore bearing one sporangium and several sporangiola. (*d*) Sporangium. (*After Schröter 1893.*)

in a dichotomous fashion, the ultimate branchlets being terminated by small few-spored sporangiola; large sporangium provided with a central, conical columella, and containing many small ellipsoidal spores unusually variable in size; sporangiolum containing only one or two large reniform spores and lacking a columella; zygospores globose, naked, formed from very unequal gametangia.

When the sporangiolum falls away the tip of the sporangiophore is seen to be provided with two or three incurved claw-like projections. These have been erroneously regarded by various workers as constituting a columella. Their true nature is elucidated by Vuillemin (1907: 33).

The genus was based on the single species, *D. fulva* Schröter, found on *Paxillus* in Baden. Another collected by Thaxter

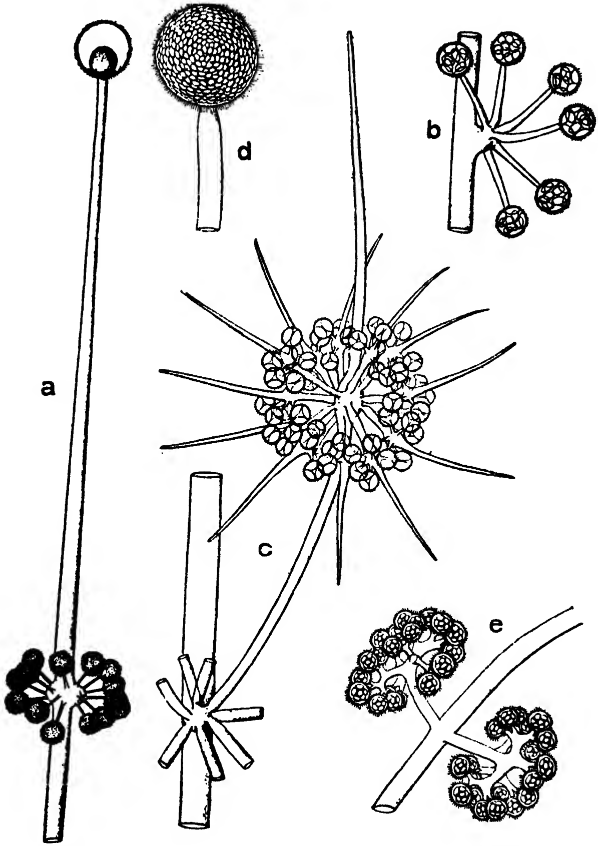

FIG. 90.—(*a, b*) *Thamnidium simplex* Brefeld, showing terminal sporangium and lateral sporangiola. (*c, d*) *Th. fresenii* Schröter, showing terminal sporangium, sporangiola, and sterile spines. (*e*) *Th. elegans* Link showing sporangiola. (*After Brefeld 1881, 1891.*)

on *Boletus* in Maine is discussed by Blakeslee (1904: 300) but is not named. The genus is of unusual interest on account of the dimorphism of spores in the two sorts of sporangia.

2. **Thamnidium** Link (*Berl. Mag. Naturf. Freunde,* **3**: 31, 1809).
syn. *Helicostylum* Corda p. p. (*Icon. Fung.,* **5**: 18, 55, 1842).
Bulbothamnidium Klein p. p. (1870: 557).
Chaetostylum van Tieghem & le Monnier p. p. (1873: 328).

Sporangiophore erect, consisting of a cylindrical central axis, usually terminated by a single, large, many-spored sporangium, and lateral branches bearing numerous, small, few-spored sporangiola (Fig. 90); lateral branches usually several times divided; the ultimate branchlets straight or circinate, terminating in sporangiola, or tapering into sterile spines; sporangium provided with a prominent columella; sporangiolum lacking a columella, containing one to twenty or more (usually about four) spores; spores alike in both sorts of sporangia; zygospores as far as known formed as in *Mucor* from approximately equal gametangia.

Individual sporangiophores, bearing only sporangiola, and others, bearing only the terminal sporangium, are not infrequently encountered. Three subgenera are recognized here.

Subgenus **Euthamnidium** Schröter (1893: 127).

Lateral branches of the sporangiophore typically dichotomously branched, the ultimate branchlets not circinate and usually all bearing sporangiola. About a half dozen species are included here, of which the best known is *Th. elegans* Link.

Subgenus **Chaetostylum** (van Tieghem & le Monnier) Schröter.
syn. *Bulbothamnidium* Klein (1870: 557).

Lateral branches of the sporangiophore verticillately branched, the central axis of each successive division swollen at the point of origin of the whorl of branches, and prolonged beyond them into a sterile spine. Two or three species are placed here, including *Th. fresenii* (van Tiegh. & le Monn.) Schröter, the type of this group. (See Sumstine, 1910: 143).

Subgenus **Helicostylum** (Corda) Schröter.

Lateral branches of the sporangiophore monopodially or cymosely branched, the ultimate branches circinate; in some cases the central axis terminating in a spine as in the preceding subgenus. The species *Th. amoenum* (Preuss) Schröter [*Helicostylum elegans* Corda] and about a half dozen other species fall here.

In recognizing the above subgenera the treatment of Schröter (1893: 127) is followed. The groups were originally described as separate genera, and are given generic rank by Fischer (1892: 246). They are clearly very closely related, and intermediate species and intergrading conditions occur (Brefeld 1881: 58; Bainier 1906: 210). For descriptions of American species consult Sumstine (1910), Pound (1894), and Povah (1915). The striking beauty of the sporangiophore in the genus renders it a favorable subject for class use.

The genus *Actinomucor* Schostak. (1898: 155), placed by Lendner near *Thamnidium*, is known only from the original description. It is here regarded as a doubtful form.

Chaetocladiaceae

Sporangia and sporangiola lacking, replaced by unicellular conidia, which cover sub-terminal enlargements of branches of the conidiophore; zygospore not enclosed in a hyphal envelope.

A single genus. 1. **Chaetocladium** (Fig. 91).

1. **Chaetocladium** Fresenius (1863: 97).

Mycelium parasitic on other members of the Mucorales, wide-spreading, profusely branched; point of attachment to host hypha marked by a dense cluster of peculiar vesicular outgrowths (Burgeff, 1920); fertile hyphae repeatedly branched; the branches tapering to long, sterile, sharp-pointed tips, many of which are provided with small subterminal swellings covered with sterigmata bearing conidia; conidia globose, unicellular; zygospores globose, formed between the ends of the copulating gametangia as in *Rhizopus*.

The genus contains two species, *C. jonesii* (Berk. & Broome) Fresenius (1863: 97) [*C. fresenianum* Brefeld, 1881: 55] based on *Botrytis jonesii* Berk. & Broome (1854: 462), and *C. brefeldii* van Tieghem & le Monnier (1873: 342) based on a form which Brefeld (1872: 29) had discussed under the name *C. jonesii*. The two species are very similar, the conidia of the first being spiny at maturity and measuring six to eight microns in diameter, while those of the second are smooth and smaller (two to four microns).

The conidia of *Chaetocladium* are frequently termed monosporous sporangia or sporangiola. This terminology is based

on the work of van Tieghem and le Monnier (1873: *pl. 23, fig. 65*), who figure germination stages in *C. jonesii*. They show the rupture of the spiny wall (sporangial wall) and the escape of a smooth-walled spore. Brefeld (1881: *pl. 2, fig. 1*) made the same observation. Preceding rupture the two walls are in close contact and indistinguishable. The homology of the conidium

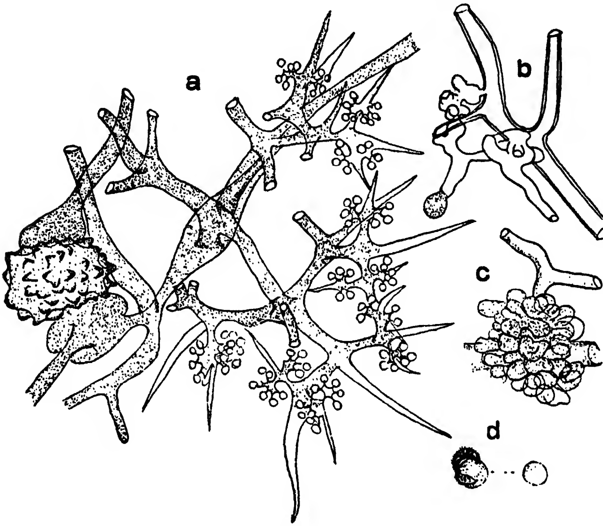

FIG. 91.—(*a–c*) *Chaetocladium brefeldii* van Tieghem & le Monnier. (*d*) *Ch. jonesii* Fresenius. (*a*) Portion of branching thallus showing conidia, sterile branchlets, and a zygospore. (*b*) Germinating conidium producing threads which are attacking a hypha of *Mucor sp.* (*c*) A cluster of short branches surrounding the host hypha in connection with haustorium formation. (*d*) Germinating conidium. (*After Brefeld 1872, 1891.*)

of this genus with the sporangium of other members of the order would have been clear, of course, even in the absence of a visible double-walled condition.

Choanephoraceae

Sporangium present in some forms, absent in others; either sporangiola or conidia present in all cases, and covering terminal capitate enlargements of branches of the sporangiophore or conidiophore.

Key to Genera of Choanephoraceae

I. Sporangium present, accompanied by either sporangiola or conidia.
   A. Sporangiola present, conidia absent; sporangiospores longitudinally striate.
      1. **Blakeslea**, p. 259
   B. Sporangiola absent; conidia present; sporangiospores not striate; conidia striate.
      2. **Choanephora**, p. 261
II. Sporangium and sporangiola absent; conidia present and echinulate, not striate
      3. **Cunninghamella**, p. 263

1 **Blakeslea** Thaxter (1914: 353).

Conidia absent; sporangia of two types (Fig. 92), larger solitary ones possessing a columella, and smaller ones termed sporangiola which lack a columella and occur in considerable numbers over the surface of large, spherical sporangioliferous heads; the two types showing, however, numerous intergrading variations; larger sporangia extremely variable in size, sometimes not larger than the sporangiola; the columella often obsolete; sporangioliferous heads sometimes solitary at the ends of erect unbranched sporangiophores, but usually in groups of ten or more and terminating branchlets of the subdichotomously branched end of the sporangiophore; sporangiolum typically three-spored, rarely four- or six-spored, attached to the sporangioliferous head by a small spherical vesicle, when mature falling away carrying the vesicle with it; spores variable in size but in general alike in all types of sporangia, longitudinally striate, provided at each end with a cluster of delicate radiating appendages like those of the sporangiospores of *Choanephora;* chlamydospores variable; zygospores where known formed between the tips of twining branches.

The genus contains a single species, *B. trispora* Thaxter, first isolated as a contamination from a *Botrytis* culture which in turn had been obtained from flowers of cowpea. It seems to occur as a weak parasite on various plants (Jochems, 1927). It has been shown by Weber and Wolf (1927) to be heterothallic. It is very closely related to *Choanephora*, differing chiefly in that the conidia of that genus are here replaced by sporangiola. The spores combine the characters of the sporangiospores and conidia of *Choanephora*, possessing the appendages of the one and the striations of the other. Thaxter (1914: 357) in a very interesting

discussion homologized the conidia of *Choanephora* with the sporangiola of *Blakeslea*, and suggests that the conidia are to be regarded as monosporous sporangiola. Although he was

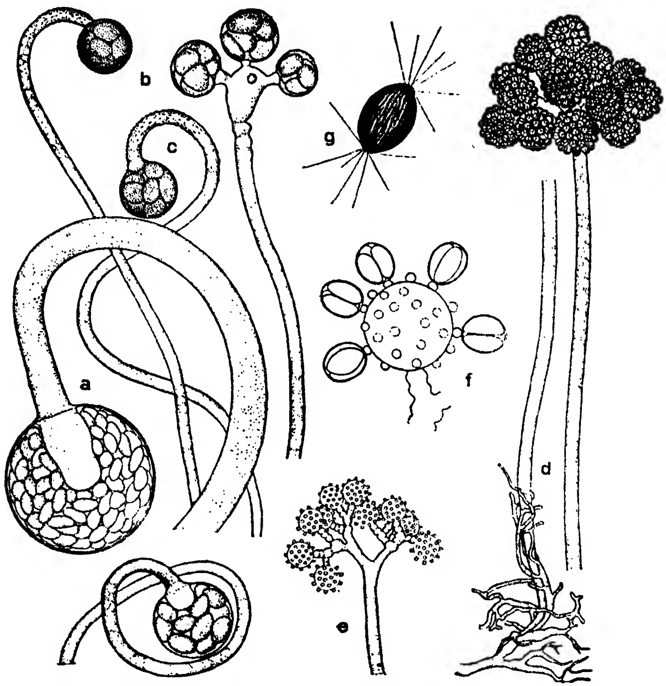

FIG. 92.—*Blakeslea trispora* Thaxter. (*a*) Typical many-spored sporangium. (*b*, *c*) Selected individuals illustrating the transition from sporangium to sporangiolum. (*d*) Typical sporangiola borne over globose heads at the apex of a fertile hypha. (*e*) Group of such globose heads denuded of sporangiola. (*f*) One head with five sporangiola attached. (*g*) A single sporangiospore. (*After Thaxter 1914.*)

unable to separate mechanically an outer thin sporangial wall from the conidia of *Choanephora* he figures somewhat abnormal conidia of *C. cucurbitarum* in which its existence is indicated. In any case homology of conidia and sporangia is very evident in these genera.

2. **Choanephora** Currey (1873: 578).
syn. *Cunninghamia* Currey (1873: 334).

Both sporangia and conidia present and not infrequently arising from the same mycelium; sporangium terminal and usually pendent on the recurved end of an erect unbranched sporangiophore, provided with a definite columella which tends to be globose, and usually containing a large number of spores, though diminutive few-spored sporangia sometimes occur; sporangiospores usually ovoid to fusiform, but occasionally

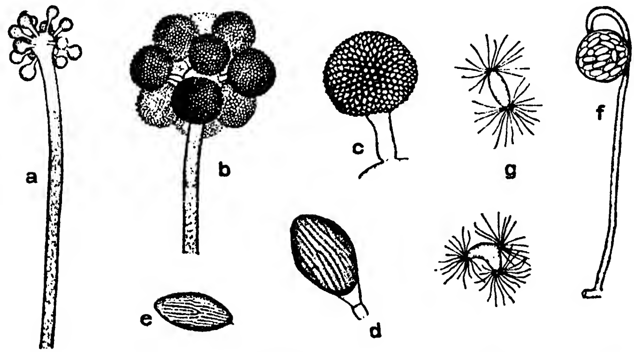

Fig. 93.—*Choanephora cucurbitarum* (Berk. & Rav.) Thaxter. (*a*) Young conidiophore with spherical heads on which conidia are just beginning to form. (*b*) Same at later stage; the heads covered with conidia borne on short sterigmata. (*c*) Single head enlarged. (*d*) Single "conidium," here shown to be in fact a mono-spored sporangiolum. (*e*) Conidium of more usual aspect; the outer wall not evident. (*f*) Sporangium. (*g*) Sporangiospores; the lower atypical. (*a–e, after Thaxter 1903, 1914; f–g) after Wolf 1917.*)

varying to inequilateral or triangular, not striate like the conidia, provided at both ends, and in spores of odd shape sometimes also at the side, with a cluster of very fine, radiating appendages as in the related genus *Blakeslea;* conidiophore an erect hypha terminated in a capitate vesicle from which a few short branches emerge; these branches, usually without branching again, enlarging at their tips to form secondary vesicles, which at maturity are covered with short sterigmata bearing conidia; the conidiophore rarely unbranched and bearing the conidia on the primary enlargement somewhat as in the genus *Rhopalomyces* (Thaxter 1891: *pl. 3*); conidia resembling the sporangiospores in shape but non-ciliate, longitudinally striate, and provided at the base

with a short hyaline appendage (Thaxter, 1914: *fig. 18A*); intercalary chlamydospores with more or less thickened walls borne on the mycelium; zygospores observed in various described species (Fig. 93).

The genus *Choanephora* is of unusual interest, since in it sporangia and conidia occur together. It is most closely related to the genus *Blakeslea* in which the conidia are replaced by sporangiola. An interesting undescribed species is mentioned by Thaxter (1914: 358), which grew in culture over a period of years without producing conidia, though sporangia bearing the typical ciliated spores of this group were always present. The following species have been described:

C. infundibulifera (Currey) Sacc. (*Syll. Fung.*, **9**: 339, 1891).
syn. *Cunninghamia infundibulifera* Currey (1873: 334).
Choanephora cunninghamiana Currey (1873: 578).

First reported from material collected in India by Cunningham on faded flowers of *Hibiscus;* also collected by Thaxter (1914: 360) from flowers of the same host in the West Indies and South America. The secondary heads of the conidiophores are persistent, and become cupulate after the conidia have fallen.

C. simsoni Cunningham (1895: 169).
Collected in India on *Ipomoea* and *Zinnia.*

C. cucurbitarum (Berk. & Rav.) Thaxter (1903: 102).
syn. *Rhopalomyces cucurbitarum* Berk. & Rav. (*Grevillea*, **3**: 11, 1875); see Thaxter (1891: 20).
C. americana Möller (1901: 18).

Reported on fading flowers of *Hibiscus, Cucumis, Gossypium, Capsicum* etc. (Dastur, 1920; Wolf, 1917; Möller, 1901; Thaxter, 1903; 1914). It is parasitic on summer squash (Wolf, 1917). An undescribed species closely related to *C. cucurbitarum,* but differing in possessing smooth conidia of a lighter color, was collected on flowers of Cucurbitaceae in South America by Thaxter (1914: 361).

C. persicaria Eddy (1925: 207).
A species, closely related to the preceding, and found recently causing a rot of peaches.

C. conjuncta Couch (1925).
A dioecious species.

Saito and Naganishi described in 1915 under the name, *Cunninghamella mandshurica,* a species whose affinities seem to be quite as much with *Choanephora* as with *Cunninghamella.* Only conidia are known, and these are longitudinally striate and identical in aspect with those of *Choanephora.* The conidiophore is of a somewhat intermediate type of branching, there being no

appreciable enlargement of the primary stalk at the point of origin of the conidia-bearing branches.

Gandrup (1923) mentions a new species, *Choanephora dichotoma*, but does not describe it.

3. **Cunninghamella** Matruchot (*Saccardo Syll. Fung.*, **6**: 508, 1905; *nom. nud. Ann. Mycol.*, **1**: 46, 1903).
syn. *Actinocephalum* Saito (*Bot. Mag. Tokyo*, **19**: 1, 1904).

Sporangia never observed in the genus, though perhaps occasionally developed under special conditions of environment (Thaxter, 1914: 358); asexual reproduction, as far as known, taking place exclusively by means of conidia (Fig. 94); conidiophores arising from the vegetative hyphae, erect, more or less branched, sometimes septate; each branch terminated in a capitate vesicle covered with sterigmata bearing small, spiny, unicellular, globose to oval or pyriform, deciduous conidia; the type of branching differing in the various species; in *C. elegans* a main stalk bearing a subterminal whorl of branches each of which is apically swollen; in *C. echinulata* the branching cymose to indefinite; globose chlamydospores intercalary in the mycelium; the known species heterothallic; gametangia approximately equal; zygospore rough but not appendaged.

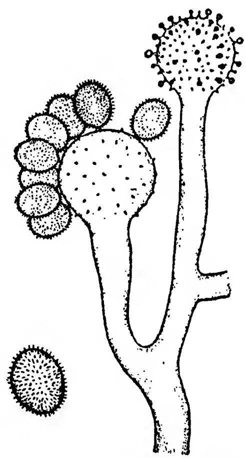

FIG. 94.—*Cunninghamella echinulata* Thaxter. Showing echinulate conidia covering capitate terminations of the conidiophore. (*After Thaxter 1891.*)

The type species of the genus was originally described by Thaxter (1891: 17) as *Oedocephalum echinulatum*. Its inclusion in this hyphomycetous genus was questioned by Matruchot (1903: 46) inasmuch as its hyphae are characteristically coenocytic, and in an interesting experiment he demonstrated that it will serve as a host for the species of *Piptocephalis* which parasitize Mucorales exclusively. He established the genus *Cunninghamella* for its inclusion and renamed the species *C. africana*. Though he failed to give a generic description, this was later

provided by Saccardo (*Syll. Fung.*, **6**: 508, 1905) and attributed to him. Blakeslee (1905: 161) further justified the inclusion of the species in the Mucorales by discovering its zygospores. Thaxter (1903: 98) pointed out that the species should bear the name *C. echinulata* Thaxter. The following additional species have been described.

C. elegans Lendner [*Bul. Herbier Boissier* (2 ser.), **5**: 250, 1907; also Mucorinées de la Suisse p. 159, 1908]. The genus *Actinocephalum* Saito, cited above as a synonym of *Cunninghamella*, was based on a single species, *A. japonicum*, which is clearly very close to *C. elegans*.

C. bertholletiae Stadel (1911).

C. blakesleeana Lendner (1928).

C. mandshurica Saito & Naganishi. Discussed above under *Choanephora*.

C. albida (Sacc.) Matruchot (1903: 56). This species, based on *Oedocephalum albidum* Sacc. (Michelia, **2**: 288, and Fungi Italici, *fig. 805*), and the following based on *Gonatobotrys microspora* Rivolta were tentatively incorporated in *Cunninghamella* by Matruchot but were not recognized by Saccardo. They may be listed as doubtful.

C. microspora (Rivolta) Matruchot (1903: 56).

Another species is mentioned but not named by Blakeslee, Cartledge, and Welch (1921).

For a discussion of zygospore formation in the genus consult their paper and that of Burger (1919).

The genera *Sigmoideomyces* Thaxter (1891: 22) and *Thamnocephalis* Blakeslee (1905: 165), known only in their conidial stages, may be listed as doubtful members of the order, but in the absence of zygospores cannot be certainly included. If incorporated they would fall somewhere in the general vicinity of *Cunninghamella*.

Mortierellaceae

Multispored sporangium present in some forms, lacking in others, when present lacking a columella; sporangiola and conidia formed in some genera, when present isolated, not covering an enlargement on the sporangiophore or conidiophore; zygospore where known enveloped in a thick layer of interwoven hyphae.

Key to Genera of Mortierellaceae

I. Sporangium present, sometimes accompanied by conidia.
   A. Sporangiophore arising directly from the ordinary mycelial hyphae.
      1. Sporangiophore erect, usually tapering to a delicate, hair-like tip beneath the sporangium, more or less swollen toward

the base; conidia unicellular, globose, echinulate, borne apically on simple or branched conidiophores; zygospore enveloped at maturity in a thick layer of closely woven hyphae.

1. **Mortierella**, p. 265

2. Sporangiophore procumbent, of uniform diameter throughout, sympodially branched.

2. **Herpocladium**, p. 268

B. Sporangiophores arising from a highly specialized, stout, creeping fertile hypha, and successively produced as buds behind its advancing tip.

3. **Dissophora**, p. 268

II. Sporangium absent, replaced by mono- or bispored sporangiola which are borne terminally and sometimes also laterally on short branches which radiate from fertile intercalary segments of the mycelium.

4. **Haplosporangium**, p. 268

1. **Mortierella** Coemans (1863: 536).

Mycelium procumbent, within the upper layer of the medium or forming a tightly appressed weft over its surface, not typically aerial; sporangiophores erect, simple, or variously and characteristically branched, usually tapering to a delicate hair-like tip just below the sporangium, and more or less swollen or ventricose downwards; sporangia globose, lacking a columella, provided with a delicate wall which disappears soon after reaching maturity, leaving only a remnant at the pointed apex of the sporangiophore; conidia (by several writers here termed **stylospores**) unicellular, globose, echinulate, occurring at the tips of simple or branched aerial conidiophores in various species, and recalling the monospored sporangia of *Haplosporangium decipiens;* zygospores enveloped at maturity in a thick layer of closely woven hyphae, which arise immediately below the gametangia and tend to obscure the conjugation process (Fig. 95).

The species of the genus, about thirty in number, are for the most part saprophytes on dung, humus, fruit bodies of higher fungi, etc. A few are facultative parasites. They are known chiefly from Europe, the genus having received little attention in America (Kauffman, 1920). The best taxonomic treatment of the group is that of Dauphin (1908).

Thaxter (1922: 291) has brought together under the provisional name Endogoneae several as yet imperfectly understood genera which show in certain respects indication of relationship with *Mortierella*. The genera included are *Endogone* Link, (*Glomus* Tulasne), *Sphaerocreas* Sacc. & Ellis, *Sclerocystis*

Berk. & Br. (*Xenomyces* Cesati, *Ackermannia* Pat.), and *Glaziella* Berk. (*Endogonella* v. Höhnel.) The genus *Endogone* (see Bucholtz, 1912: 147) is the largest and most interesting member of the group (Fig. 96). In certain of its species thick-walled zygospores are produced in compact groups, the whole mass usually being enclosed in a hyphal envelope. A definite fruit body thus results which recalls on the one hand the zygosporic

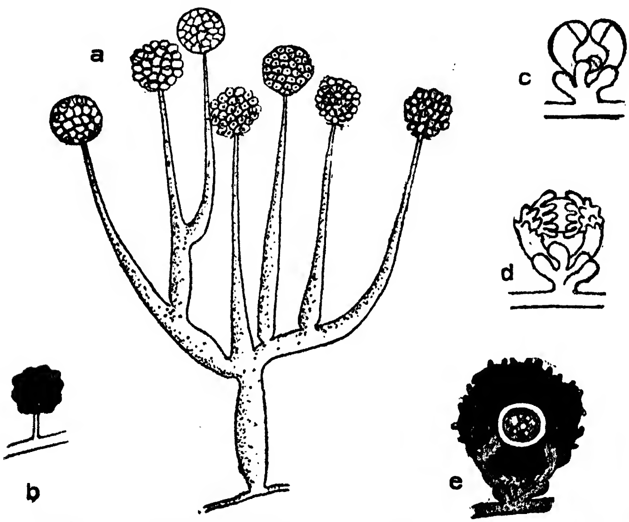

FIG. 95.—(*a*) *Mortierella candelabrum* v. Tiegham & le Monnier, showing branching sporangiophore. (*b*) *M. fusispora* v. Tieghem. "Stylospore" (conidium). (*c–e*) *M. nigrescens* v. Tieghem, showing successive stages in zygospore formation. (*After v. Tieghem and le Monnier 1873, 1876.*)

envelope of *Mortierella* and on the other the more definite fruit body of the Ascomycetes. In other species of the genus the interior of the fruit body is filled with azygospores (chlamydospores), and in still others with sporangia. In one known species zygospores and chlamydospores occur together, but neither of these spore forms has been found in any of the sporangia-producing species. The sporangia resemble those of *Mortierella*. The zygospore is formed in a bud put out by the fusion cell which results from the copulation of the gametangia, and appears to surmount them. Thus, though resembling *Mortierella* in

possessing an envelope, it shows an essential relationship with species of the Piptocephalaceae. The zygospores and chlamydospores have never been seen to germinate, but sporangial germination has been observed (Walker, 1923: 245). The genus has been considerably misunderstood, the term ascus having been applied to the sporangium as well as to the zygospore and chlamydospore by various authors. Atkinson (1918: 1) regarded the genus as constituting an interesting type between the Zygomycetes and the Protoascomycetes, and states that it affords

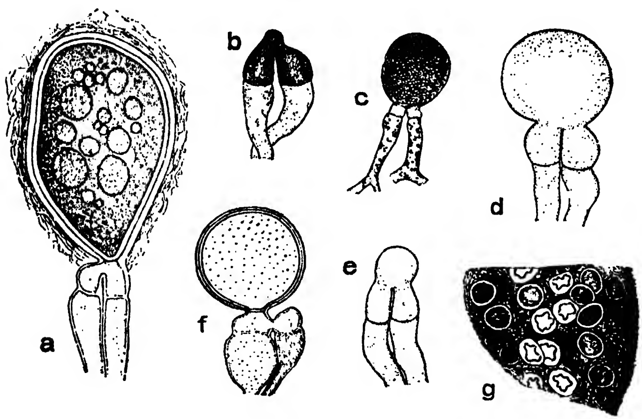

FIG. 96.—*Endogone spp.* (*a*) Zygospore; its origin from gametangia, and enveloping hyphae of sporocarp (fruit body) shown. (*b–f*) Stages in zygospore formation. (*g*) Portion of sporocarp in section showing peridium and spores, some of the latter immature. (*After Thaxter 1922.*)

strong evidence of the Phycomycete ancestry of the Ascomycetes. The genera *Sphaerocreas, Sclerocystis,* and *Glaziella,* known only in the chlamydospore condition, resemble the chlamydospore-producing species of *Endogone* sufficiently to indicate a relationship between the various genera. They differ chiefly in minor structural features of the fruit body. Whether these four genera should be regarded as constituting a separate family of the Mucorales related to and somewhat higher than the Mortierellaceae is perhaps open to question, but in the present state of knowledge it seems very likely that the group should be incorporated in the Mucorales.

2. **Herpocladium** Schröter (1886: 213).
syn. *Herpocladiella* Schröter (1893: 130).

Mycelial characters unknown; sporangiophore of equal diameter throughout, sympodially branched, winding about over the substratum for a considerable distance, not erect; sporangia terminating the branches, globose, lacking a columella and with a transitory wall as in *Mortierella;* zygospores unknown.

A doubtful monotypic genus based on a little known species, *H. circinans* Schröter. This genus and *Mortierella* compose the family Mortierellaceae of Schröter. They are similar in sporangial characters but seem to have little else in common and may prove on further study to be unrelated.

The name *Herpocladium* was changed by Schröter to *Herpocladiella,* on account of the existence elsewhere of a subgenus bearing the former name.

3. **Dissophora** Thaxter (1914: 361).

A monotypic genus, based on *D. decumbens* Thaxter (Fig. 97); sporangia and sporangiophores as in *Mortierella;* fertile hypha unlike those of other genera of the order, at first erect, then falling over and creeping over the substratum, stout; abruptly differentiated from the slender vegetative hyphae, producing sporangiophores which arise as buds successively produced behind its advancing tip; fertile hyphae and sporangiophores septate; zygospores unknown.

4. **Haplosporangium** Thaxter (1914: 362).

Resembling *Dissophora* in the possession of highly specialized structures from which the sporangiophores arise, but these structures consisting of prostrate, intercalary, septate segments of the mycelium; sporangiophores borne without regularity on all sides of the fertile segment and radiating from it, short, stout, tapering to hair-like tips bearing the sporangiola, sometimes branching slightly and bearing lateral sporangiola also; sporangiola very minute, containing only one or two spores; columella lacking; zygospores unknown (Fig. 98).

In general aspect the fungi included here resemble certain Hyphomycetes such as *Hyalopus* or *Cephalosporium,* and may be easily mistaken for them. The genus includes only the two species on which it was erected. In one of these, *H. bisporale* Thaxter, the sporangiolum usually contains two spores, though

sometimes only one. In the second species, *H. decipiens* Thaxter, one-spored sporangiola only have been observed. In the latter

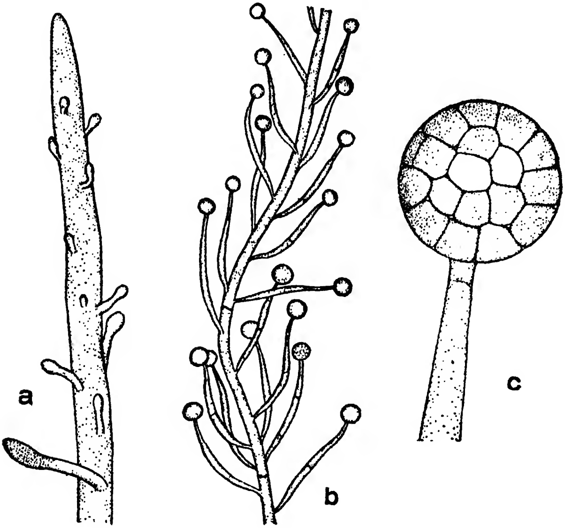

FIG. 97.—*Dissophora decumbens* Thaxter. (*a*) Terminal portion of fertile hypha showing origin of sporangiophores behind the elongating apex. (*b*) Portion of fertile hypha bearing mature sporangiophores. (*c*) Mature sporangium. (*After Thaxter 1914.*)

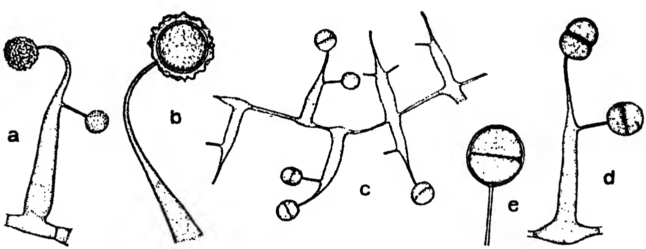

FIG. 98.—(*a, b*) *Haplosporangium decipiens* Thaxter, showing monosporic sporangiola. (*c–e*) *H. bisporale* Thaxter with bisporic sporangiola. (*After Thaxter 1914.*)

case the wall of the sporangiolum is roughened while that of the enclosed spore is smooth.

Thaxter regards the genus as closely related to *Mortierella*. Torrey (1921) regards the 1-spored sporangiola of *Haplosporangium* as equivalent to the conidia ("stylospores") of *Mortierella*. He then arranges a phylogenetic line in which *H. bisporale* ("with sporangiola and stylospores") lies between *H. decipiens* ("with only stylospores") on the one hand, and *Mortierella* ("with sporangia and stylospores") on the other.

Piptocephalidaceae

Sporangium narrowly cylindrical or rod-like, relatively few-spored; sporangiospores standing in a single row, at maturity having the aspect of a chain of conidia due to the dissolution of the sporangial wall; zygospore usually formed in a bud put out by the fusion cell resulting from the copulation of the gametangia, not enveloped in a layer of hyphae.

Key to Genera of Piptocephalidaceae

I. Fertile sporangiferous hypha branched.
   A. Branching dichotomous or pseudodichotomous in type.
      1. Some of the branches prolonged into sterile prongs; sporangiferous heads not deciduous.
         1. **Dispira**, p. 270
      2. All the branches terminating in sporangiferous heads; the latter deciduous.
         2. **Piptocephalis**, p. 272
   B. Branching cymose to indefinite, not dichotomous, sporangiferous heads not deciduous.
         3. **Syncephalastrum**, p. 273

II. Fertile sporangiferous hypha not branched below the terminal enlargement; provided with spur-like rhizoids at the point of attachment with the substratum.
         4. **Syncephalis**, p. 273

1. **Dispira** van Tieghem (1875: 160, *fig. 173–177*).

Mycelium parasitic on other Mucorales; sporangiophores erect, repeatedly branched in a dichotomous or pseudodichotomous fashion; each successive branch delimited by a septum at its base; some of the terminal branches tapering into curved, sterile, sharp-pointed tips; the others swollen to form spherical heads over which numerous sterigmata arise bearing cylindrical sporangia; each sterigma consisting of a single cell with a transverse median constriction or of two superimposed cells, the terminal one of which buds from the lower; sporangium containing a

single row of spores (six in *D. cornuta* van Tieg., two in *D. americana* Thaxter) which at maturity have the aspect of a chain of conidia due to the dissolution of the sporangial wall; zygospores formed in an anomalous manner and always in close connection with the host hypha; at maturity partly enclosed by finger-like processes which arise from one of the gametangia (Fig. 99).

The points of dissimilarity between the two above named species, as indicated by the original descriptions, are enumerated by Thaxter (1895: 513). More recently Bainier (1906: 213)

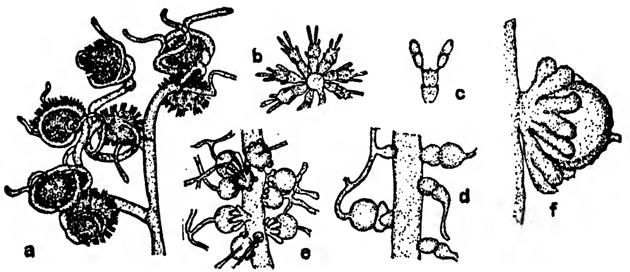

FIG. 99.—*Dispira americana* Thaxter. (*a*) Sporangiophore with spherical sporangium-bearing heads and sterile sharp-pointed tips. (*b*) Optical section of a single such head showing the peculiar budding sterigmata terminated by sporangia. (*c*) Sterigma bearing two sporangia, each containing two spores. (*d*) Sporangiophore of *Mucor* attacked by hyphae of *Dispira;* the latter septate near host hypha to form pairs of gametangia. (*e*) Gametangia and zygospores in various stages of development. (*f*) Single mature zygospore surrounded in part by a rosette of finger-like processes arising from one of the gametangia. (*After Thaxter 1895.*)

has redescribed *D. cornuta* and states that the two species are identical. A third species, *D. circinata* Elliott (1926) has been described rather inadequately from the asexual stage only.

The sexual process as described by Thaxter for *D. americana,* may be briefly reviewed. From the slender creeping vegetative hyphae of the parasite short lateral branches are put out which come in contact with the host hypha and attach themselves to it as suckers. Each sucker then becomes septate into two cells which then function as gametangia in zygospore formation. The enveloping finger-like processes always arise from that gametangium which joins the host.

Although in *Dispira* the chains of spores developed at the tips of the fertile hyphae have not been demonstrated clearly

to be endogenous in character, they are here so regarded from analogy with those of the other genera incorporated in the family.

Several other genera, known only in the asexual stage, apparently belong near *Dispira*. One of these, *Dimargaris* van Tieghem (1875: 154, *figs. 165–172*), a monotypic genus based on *D. cristalligena*, possesses fertile hyphae so strikingly similar to those of *Dispira americana* that discovery of intermediate species would necessitate the merging of the two genera. The other genera are *Kickxella* Coemans (1862: 155) [*Coemansiella* Saccardo, *Sylloge Fungorum*, **2**: 815], *Martensella* Coemans (1863: 536), *Spinalis* Vuillemin (1904 *b*: 26), *Saitomyces* Ricker (*Jour. Mycol.*, **12**: 61, 1906), and *Coemansia* van Tieghem & le Monnier (1873: 392).

2. **Piptocephalis** de Bary (1866: 356).

Mycelium parasitic on other Mucorales, running over the host hyphae and attached to them at intervals by swollen suckers from which delicate, filamentous haustoria penetrate the host cell; fertile hyphae erect, cylindrical, septate, repeatedly dichotomously branched; ultimate branches terminally more or less swollen to form deciduous capitate enlargements over whose surface sterigmata project bearing cylindrical rod-like sporangia; sporangia at maturity forming simultaneously a single row of spores which appear, after the dissolution of the sporangial wall, as a row of conidia; in one species, *P. monospora* Mangin (1899: 376), the sporangium containing only a single spore, in another, *P. microcephala* van Tieghem (1875: 148), only two; zygospore globose, rough, formed by the enlargement of a bud which develops from the point of union of two clavate gametangia which come in contact at their apices after the fashion of a pair of tongs (Fig. 100).

About a dozen species have been described, the majority by van Tieghem (1875: 137). No recent monograph of the genus has appeared, the best general treatment being that of Fischer (1892: 287).

An unusual interpretation of the homologies of the asexual stage in this genus and the others of the family is given by Gäumann (1926: 103). He regards the capitate enlargement at the apex of the fertile hypha as the sporangium, and terms the cylindrical branches in which the spores are borne **extrasporangial partial sporangia.** His point of view is the same with respect

to *Blakeslea* which he regards as a connecting form in a phylogenetic series embracing *Choanephora* and *Cunninghamella* on the one hand and *Piptocephalis, Syncephalis,* and *Syncephalastrum* on the other.

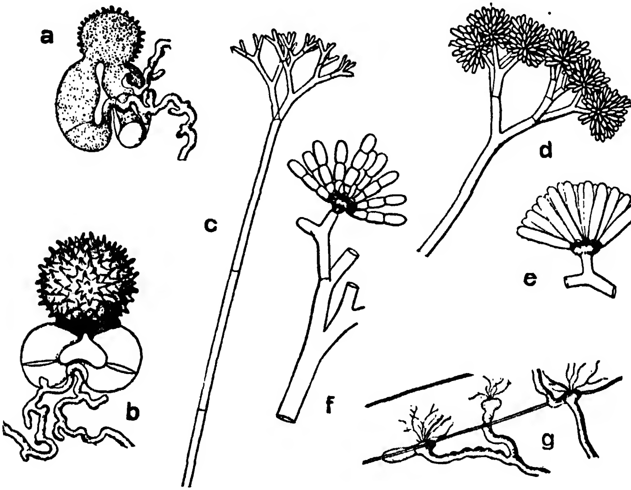

FIG. 100.—*Piptocephalis freseniana* de Bary (*a, b*) Zygospore formation. (*c–f*) Steps in the process which results in the formation of chains of sporangiospores. (*g*) Mycelium attached to host hypha and sending rhizoids into it. (*After Brefeld 1872.*)

3. **Syncephalastrum** Schröter (1886: 217).

Mycelium wide-spreading, abundantly branched; sporangiophore erect, lacking basal rhizoids, repeatedly branched, each branch apically dilated to form a globose head bearing rod-shaped sporangia on sterigmata; sporangiospores formed simultaneously and assuming the aspect of chains of conidia as in related genera; zygospores unknown (Fig. 101).

About six or seven species are known. Although the members of the genus are typically saprophytic, a species has been recently described by Vuillemin (1922: 986) as parasitic on *Rhizopus*.

4. **Syncephalis** van Tieghem & le Monnier (1873: 372).

Mycelium parasitic on other Mucorales or saprophytic, attached to the host hypha by suckers and sending in delicate

thread-like haustoria as in *Piptocephalis;* fertile hyphae erect, straight or apically uncinate, provided at the base with prominent rhizoids, apically dilated to form a clavate to globose enlargement, which in some species bears rod-like sporangia directly on sterigmata, but in other forms more or less elongate branches which are provided at the tips with sterigmata bearing the sporangia; number of spores in a sporangium more or less

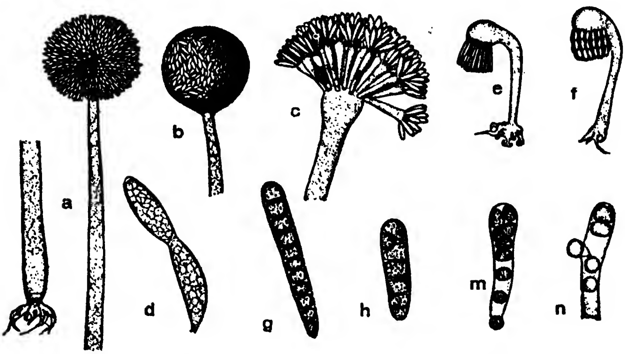

FIG. 101.—(*a–d*) *Syncephalis wynneae* Thaxter. (*e, f*) *Syncephalis reflexa* v. Tieghem. (*g, h, m, n*) *Syncephalastrum racemosum* Cohn. *a.* Fertile hypha with spur-like rhizoids at base and spores still *in situ* at apex. (*b*) Spores freed from sporangia adhering in a viscous spherical mass. (*c*) Enlarged apex of fertile hypha from which radiate branches terminated by clusters of tubular sporangia. (*d*) One such sporangium with its pair of spores nearly mature. (*e, f*) Sporangia before and after spore formation. (*g*) Normal sporangium containing single row of mature spores. (*h*) Sporangium containing one lateral spore. (*m*) Spores escaping through base of a detached sporangium. (*n*) Crushed sporangium. (*After Thaxter 1897.*)

definite in a given species, in some species only two or three; spores at maturity assuming the aspect of a chain of conidia; under moist conditions all the spores on a head held together as a spherical mass in a droplet of water; zygospores formed somewhat as in *Piptocephalis,* conjugating branches more or less coiled about each other (Fig. 101).

The genus contains about twenty-five species. The most extensive taxonomic treatments are those of van Tieghem (1875: 114–137) and Fischer (1892: 295). An interesting discussion of the genus is given by Thaxter (1897: 1).

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CHAPTER X

ENTOMOPHTHORALES

Mycelium is less profusely developed in this order than in the Mucorales, and is more characteristically septate. Though in a few species it persists to maturity as a filamentous branching thallus, there is the tendency in the majority of forms for the hyphae to be limited in development and to fall apart early at the septa into the component cells. These hyphal segments are then termed **hyphal bodies.** They increase in number rapidly by fission and budding. The cells of the thallus are usually plurinucleate, but in the genus *Basidiobolus* are typically uninucleate.

The majority of species are parasitic on insects, and relatively few of these have ever been obtained in culture on artificial media. Consequently, obligate parasitism has been assumed to be predominant in the group. In recent years some degree of success has attended attempts to get these forms in culture, and it now seems probable that many of them will be found to develop saprophytically when favorable media are provided (Sawyer, 1929). Although the group is chiefly entomogenous a few species are parasitic on plants, and several forms are true saprophytes wholly lacking in parasitic tendencies.

In asexual reproduction **conidia** are abjointed at the tips of simple or indefinitely branched clavate conidiophores, and, except in *Massospora*, are forcibly discharged, the phenomenon being strikingly similar to that exhibited in *Pilobolus* of the preceding order, where a multispored sporangium is shot away. The conidium is in all cases unicellular, and is assumed to be the homologue of the sporangium present in preceding groups. In *Basidiobolus*, in the case of one of the two species comprising the genus, it has been shown recently that the "conidium," after being ejected, functions as a sporangium by the production of endogenous spores. In all other cases, as far as known, the conidium germinates by a tube, which grows directly into mycelium or cuts off a secondary conidium which is in turn

discharged. The almost total suppression of sporangiospore formation, coupled with the presence of the phenomenon of discharge, indicates that the asexual stage in this order has reached a higher point in development than is seen elsewhere in the Phycomycetes. The conidiophore arises as an outgrowth from a cell of the filamentous mycelium or from a hyphal body and, except in *Massospora,* pushes through the host tissue or substratum to the surface, where it forms its conidia in the air. The conidiophores stand finally in tufts or in a definite palisade layer or hymenium which may cover a considerable area. In *Massospora* the conidia reach maturity within the host and fall away from the condiophores instead of being discharged.

The hyphal bodies sometimes assume thick walls and function as **chlamydospores.** Definite globose, thick-walled resting spores (**zygospores** or **azygospores**) are formed in most species. Zygospores result from a true sexual conjugation of a pair of hyphal bodies or cells of the filamentous mycelium. Azygospores are formed without conjugation from one such cell. These resting spores are formed either within one of the fusing cells (*Basidiobolus, Conidiobolus*) or in an outgrowth or bud from one of the cells or from the canal at their point of union as in *Piptocephalis* of the preceding order. Little is known concerning germination of the resting spore in the group. It probably puts out a tube which functions as a conidiophore or grows directly into mycelium.

The order as here treated consists of the single family Entomophthoraceae, including five genera. The genus *Basidiobolus* was removed from this family by Gäumann (1926), and made the basis of another family Basidiobolaceae. Later Gäumann and Dodge (1928) incorporated all the forms in the single family Entomophthoraceae but recognized two subfamilies, Basidioboleae and Entomophthoreae. Lakon (1926) emphasizes the desirability of retaining *Basidiobolus* in the family on account of intergrading characters in various forms. The writer feels that little if anything is to be gained by splitting the group.

No general monograph of the species of the world has yet been prepared. The paper on American forms by Thaxter (1888) is the most extensive discussion of the group, and is excellently illustrated.

The most widely distributed and generally known species of the order is *Empusa muscae,* parasitic in the house fly. In late summer and autumn flies attacked by this fungus may be seen,

held fast to the window pane by the tip of the proboscis, and are easily identified by the whitish halo of conidia which lie on the glass surrounding them.

Key to Genera of Entomophthoraceae

I. Mycelium not entomogenous (*i.e.*, not living in insects).
  A. Mycelium profusely developed, not intracellular.
    1. The asexual reproductive cell finally forming endogenous spores, hence termed a sporangium; apical portion of sporangiophore immediately below the sporangium differentiated as a peculiar conical "basidium," which is shot away with the sporangium; saprophytes.
      1. **Basidiobolus, p. 283**
    2. The asexual reproductive cell functioning as a conidium; a specialized "basidium" absent; conidium freed from the conidiophore completely as in *Empusa;* parasites or saprophytes.
      2. **Conidiobolus, p. 286**
  B. Mycelium only slightly developed, intracellular, parasitic in fern prothallia.
      3. **Completoria, p. 288**

II. Mycelium entomogenous.
  A. Conidia borne within the body of the host, and freed by its disintegration, not shot away, verrucose.
      4. **Massospora, p. 289**
  B. Conidia borne on the surface of the host, smooth-walled, discharged forcibly from the conidiophore.
      5. **Empusa, p. 292**

1. **Basidiobolus** Eidam (1886: 194).

As founded by Eidam the genus *Basidiobolus* embraced two species, *B. ranarum* Eidam and *B. lacertae* Eidam, the first saprophytic in nature on the excrement of frogs, the second on that of lizards. Later another species, *B. myxophilus* R. E. Fries (1899), was isolated from fallen pine needles, where it was found associated with a slimy bacterial exudation. An extensive discussion of the morphology and taxonomy of the genus was given by Eidam, and soon afterward Thaxter (1888) published notes on American material of *B. ranarum*. More recent studies (*e.g.*, Levisohn, 1927) indicate that the two species of Eidam are identical. If this point of view is accepted the organism should bear the name *B. ranarum*. The species has been studied cytologically by Eidam, Fairchild (1897), Woycicki (1904; 1927), Olive (1907), and Levisohn. In it, zygospore formation is of an

unusual type, and interesting in connection with any consideration of the phylogeny of the order. In a sense the genus may be said to be intermediate in type between the Oomycetes and Zygomycetes.

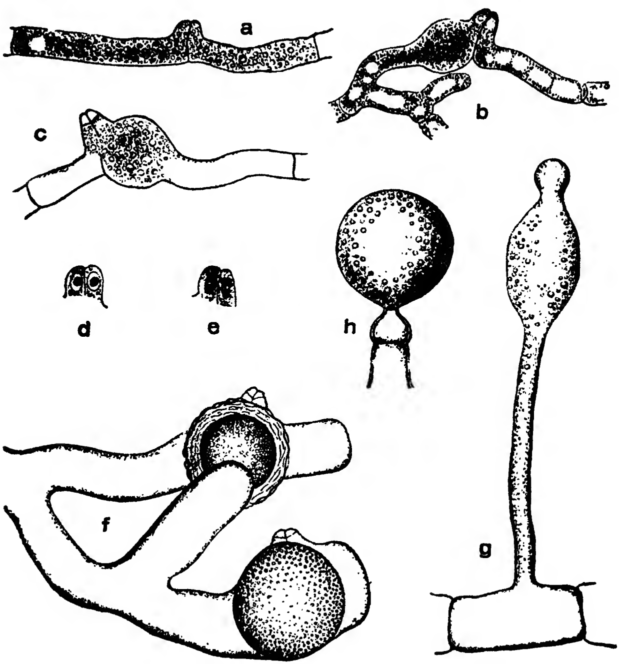

FIG. 102.—*Basidiobolus ranarum* Eidam. (*a*) Formation of beaks. (*b*) Nuclei in beaks. (*c*) Beaks septate. (*d*, *e*) Nuclear division in beaks. (*f*) Zygospores. (*g*, *h*) Conidial formation. (*a–e, after Eidam 1886; f, h, after Thaxter 1888.*)

In *B. ranarum* (Fig. 102) the mycelium develops profusely on the excrement, and consists of branching threads which in nature retain their hyphal form. They are composed normally of uninucleate cells, though in age or under conditions of unsatisfactory nutrition they may become multinucleate. The fungus grows well in culture on various artificial media, but in culture may

break up into oidia, which are regarded as comparable to the hyphal bodies commonly developed elsewhere in the family.

In asexual reproduction, slender erect sporangiophores are raised above the substratum, each becoming apically inflated to form a clavate termination recalling the subsporangial vesicle of *Pilobolus*. From this a terminal bud is put out which enlarges into a pyriform sporangium ("conidium"). The sporangium is uninucleate, and finally is discharged with violence from the sporangiophore. Preceding discharge a portion of the tip of the subsporangial vesicle is differentiated by contraction and the assumption of a thicker wall to form a conical structure, termed the "basidium," immediately beneath the sporangium. This "basidium" is carried away with the sporangium when discharge occurs, rupture of the apex of the subsporangial vesicle being transverse. Later the two fall apart. At the time of discharge sporangiospores have not yet been formed.

Until very recently the phase of the life cycle of *B. ranarum* which precedes the appearance of the mycelium in the excrement was wholly unknown. In an able investigation Levisohn (1927) has now shown that the sporangia, after being shot away from the sporangiophore, are eaten by beetles, and that these in turn are devoured by frogs. In the alimentary tract of the frog the sporangium undergoes further development. Its nucleus divides several times, and thin-walled non-motile sporangiospores are cut out. The number is often eight. These spores escape by the disintegration of the sporangial wall, and lie free for a time in the body of the frog, multiplying there by fission. Only after reaching the outer air are they capable of germination to form mycelium. In culture under optimum conditions the sporangium germinates by forming endogenous spores, but more commonly it functions as a conidium and sends out germ tubes directly.

In age, the mycelium forms zygospores. Conjugation takes place between adjacent cells of the same hypha. Since the cells are uninucleate it is not unlikely that their nuclei are sisters. This close relationship may explain the rather peculiar and apparently unnecessary phenomenon which follows. At the point where the zygospore is to be formed a beak-like protrusion is pushed out on each side of a transverse septum. These beaks grow in lateral contact until a considerable length is attained. In each case the nucleus of the parent cell migrates out into

the beak and divides there by mitosis. One of the daughter nuclei in each beak then passes back into the parent cell, the beaks are cut off by septa, and the nuclei remaining in the beaks disintegrate. One of the parent cells then enlarges until it becomes many times the size of the other, and the septum between the cells in part disappears leaving a large pore. The nucleus of the smaller cell accompanied by the cytoplasm passes through the pore, and in the larger cell the two nuclei soon lie together and seem about to fuse. In some cases they may do so, but in others they seem to undergo a final division, after which one daughter nucleus in each case disintegrates and the remaining pair fuse. The combined cytoplasm of the two cells finally contracts about the fusion nucleus, forming a resting spore which at maturity is thick-walled and lies free in the larger cell. In several respects this process of sexual spore formation recalls that of the Oomycetes, and the spore might easily be regarded as an oospore. However, it is termed a zygospore in all the literature, and the characters of the asexual stage indicate clearly that the fungus belongs to the Zygomycetes.

The life history of the other species, *B. myxophilus* is very imperfectly known.

The genus *Ichthyophones* Plehn and Mulsow containing several species isolated from the intestinal tract and excrement of fish is very closely related to *Basidiobolus*, if not in fact actually identical with it. This is strongly indicated by figures published recently by Leger (1927) for *I. intestinalis* Leger & Hesse. The presence of globose uninucleate cells in the alimentary canal of the fish affords a point of striking similarity between the two genera, and may indicate a comparable life cycle.

2. **Conidiobolus** Brefeld (1884: 37; also see Schröter 1889: 224).

In this genus the mycelium when young is profusely developed, consisting of richly branching, many-septate threads. Later irregularly swollen or lobulated portions are put out, and these, shortly before conidiophore formation, break apart at the septa to form irregular hyphal bodies. The conidiophores are unbranched. They arise from the hyphal bodies, and cut off apically large solitary conidia which are discharged violently as in *Empusa*.

The genus was founded by Brefeld on *C. utriculosis* Brefeld and a smaller-spored form, *C. minor* Brefeld, both occurring on the fruit body of *Auricularia* as parasites or facultative sapro-

phytes. Another species studied in recent years in America by Gilbert (1919: 263) and Martin (1925 *b*: 311), and described by the latter writer as *C. villosus* Martin, was isolated from fern prothallia and from rotting wood bearing a species of *Hypochnus*. It grows readily on artificial media.

Sexual spores are known only in *C. utriculosis*. Here a pair of projections arising from two hyphal bodies enlarge terminally.

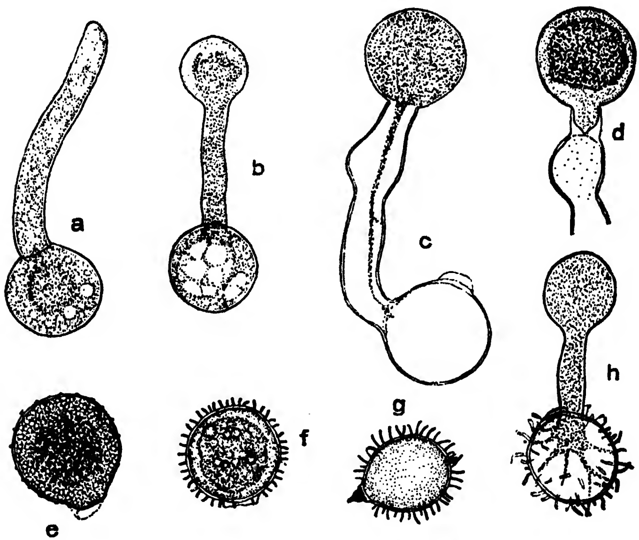

FIG. 103.—*Conidiobolus villosus* Martin. (*a–d*) Stages in germination of conidium and formation of secondary conidium. (*e, f*) Transformation of conidium into an appendaged resting spore. (*g*) Resting spore shrunken to oval form. (*h*) Germination of resting spore. (*After Martin 1925.*)

These apical swellings, which are very unequal in size, come in contact and conjugate, the intervening walls being broken down. The contents of the two cells merge, and a large, thick-walled spore is formed in one of the cells. Brefeld regarded the process as distinctly oomycetous in nature, but Thaxter feels that the spore is clearly a zygospore. In *C. villosus* (Fig. 103) the direct transformation of mature conidia into characteristically appendaged resting spores is described by Martin.

The genus *Delacroixia* Constantin (1897), known only in the conidial phase, is clearly very closely related to *Conidiobolus*. It contains the single species, *D. coronata* Constantin, found growing as a saprophyte on the gills of mushrooms and on orchid seed. Gallaud (1905) has studied the form in culture in nutrient solutions and on various solid media. Until its resting spores are discovered its position will remain somewhat in doubt.

3. **Completoria** Lohde (1874).

The genus *Completoria* contains a single species, *C. complens* Lohde, parasitic on prothallia of various ferns. It has been studied extensively by Leitgeb (1881) in Europe and by Atkinson (1894) in America.

The vegetative portion of the fungus consists of a more or less compact botryose cluster of short, oval, or somewhat curved hyphal branches originating from a common center and presenting on the surface a convoluted appearance (Fig. 104). This vegetative body is confined at first to a single host cell, and is often small and inconspicuous, being composed of only a few branches closely recurved upon the parent hyphae. At times it is larger, completely filling even a large host cell. At maturity it usually spreads to neighboring cells, certain peripheral branches merely putting out slender threads which pierce the intervening walls. Such a thread on reaching the center of the new cell cavity enlarges at its tip to form an oval body into which the protoplasm of the parent cell flows. This oval enlargement then puts out short protuberances which become enlarged at a short distance from their point of origin, undergo branching, and soon give the botryose appearance of the parent thallus.

Under certain conditions the fungus produces resting spores. They are formed in the interior of the thallus, ten or more often being found in a compact group surrounded by the smaller, terminal, then empty, peripheral branches. The resting spore is globose to oval, and at maturity is provided with a smooth, three-layered wall. Its sexual nature has not been demonstrated. Asexual reproduction by means of aerial conidia sometimes occurs. The conidia in their shape and method of formation resemble those of other members of the order, and at maturity are forcibly ejected. Inclusion of the genus in the Entomophthorales rests chiefly on a consideration of the conidial stage. The resting spore, though tentatively termed an oospore by

Atkinson has been regarded by others as a chlamydospore or azygospore.

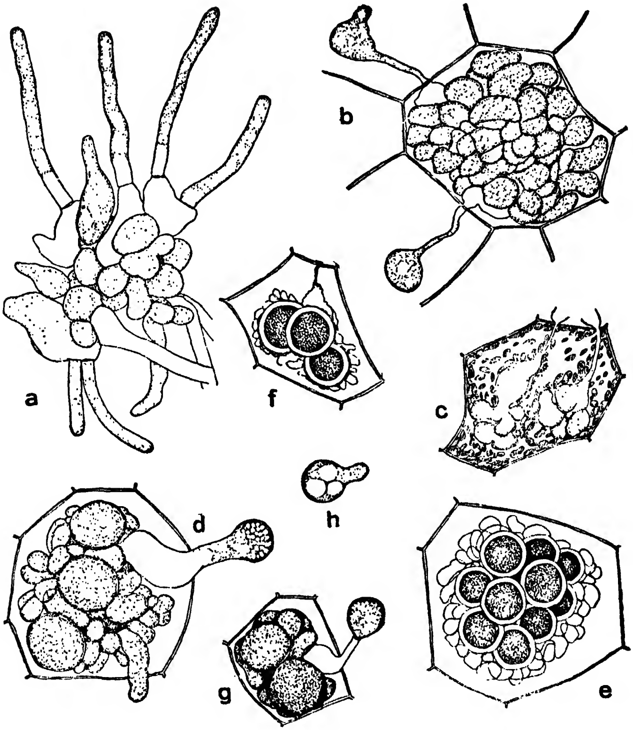

FIG. 104.—*Completoria complens* Lohde. (*a*) Botryose cluster of cells comprising the thallus. germinating in water to form long tubes. (*b*) Host cell containing the thallus of the parasite, two peripheral cells of which have developed tubes and penetrated adjacent host cells. (*c*) Two young thalli still showing attachment to penetration tubes which entered from other host cells. (*d*) Several cells of thallus forming resting spores; one developing a conidium. (*e, f*) Resting spores surrounded by empty peripheral cells. (*g*) Resting spores and a single fully formed conidium. (*h*) Germinating conidium. (*After Atkinson 1895.*)

4. Massospora Peck (1879: 44).

The genus was founded on a single species, *M. cicadina* Peck, parasitic on the seventeen-year cicada, *Tibicina septendecim.*

It was regarded by Peck as a relative of *Protomyces*, but Thaxter (1888) and Forbes (1888) working independently transferred it to the Entomophthoraceae. Their knowledge of the fungus was very imperfect, and its real nature has been elucidated only recently by Speare (1921). Though clearly a member of the Entomophthoraceae it differs from the other genera in several outstanding respects.

The vegetative growth of the fungus is confined to the softer tissues in the posterior segments of the body of the host. These segments, as a result of their complete destruction, disintegrate

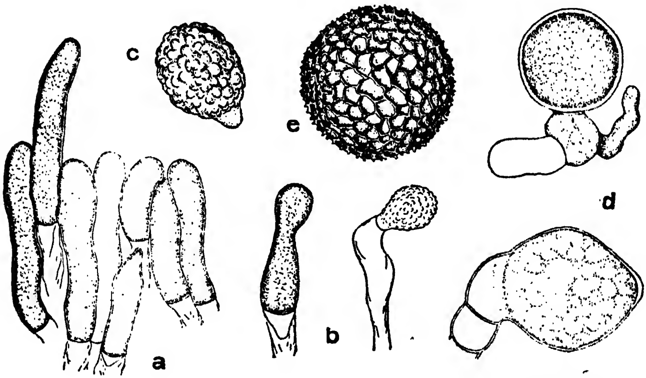

FIG. 105.—*Massospora cicadina* Peck. (*a*) Group of conidiophores. (*b*) Conidial formation. (*c*) Conidium. (*d*) Resting spores formed as buds from hyphal bodies. (*e*) Mature resting spore. (*After Speare 1921.*)

progressively forward until as much as half of the body of the insect has fallen away (Fig. 106). Meanwhile the host remains alive for a considerable period, and may fly and crawl about among its fellows. This process of sloughing off of the body of the insect is unknown in other genera of the Entomophthoraceae and is here concerned in spore dispersal. In *Massospora* the conidia are neither borne over the surface of the host nor ejected forcibly from the tips of the conidiophores. They are formed within the body of the insect (see *Amer. Jour. Bot.*, **16**: 394, 1929) and, though delimited on the conidiophore in the manner usual in this group, are held in the approximate position in which produced, finally cohering with one another to form a powdery mass of spores. They are exposed by the disintegration of the

intersegmental abdominal membranes of the host, and falling away gradually, are disseminated by the wind. The conidia, unlike those of other genera, are markedly verrucose instead of smooth (Fig. 105). The early stages of mycelial development have not yet been satisfactorily observed, but in later phases hyphal bodies are present, and give rise to conidiophores and

FIG. 106.—*Massospora cicadina* Peck on periodical cicada (*Tibicina septendecim* L.). (*a*) Portions of the anterior four abdominal segments dissected away to expose the mass of resting spores within. (*b*) The abdomen with the attached mass of conidia after considerable natural sloughing off has occurred. (*After Speare 1921.*)

resting spores. The latter are spherical, slightly brownish, and have beautifully reticulated walls. Each resting spore arises as a bud from a hyphal body and is apparently asexually produced. In the present state of knowledge these spores are to be regarded as azygospores, but a more critical study of their method of formation is desirable. No data are available bearing on the question of how the fungus passes the long period during which the host remains under ground.

Three other species have been referred in the literature to this genus. One, *M. richteri* Bresadola & Staritz (Staritz, 1892), was subsequently transferred to *Empusa* (Bubak, 1906: 105). The remaining two, *M. cleoni* Wize (1905: 716) and *M. staritzii* Bresadola (1892: 133) are so imperfectly known that their inclusion here must be regarded as merely tentative.

5. **Empusa** Cohn (1855: 301).

syn. *Entomophthora* Fresenius (1856: 882).
Lamia Nowakowski p.p. (1884: 153).
Tarichium Cohn p.p. (1875: 58).

The members of this genus are all entomogenous, and were long thought to be obligate in their parasitism. In recent years several species have been induced to grow saprophytically on artificial culture media (Sheldon, 1903; Speare, 1912; Sawyer, 1929) and it is probable that others will be obtained in culture when the proper conditions are provided.

In nature, infection of the host results when a germ tube from the conidium penetrates the outer covering of the insect and enters the body cavity. In the host the infection thread usually does not develop a profusely branching mycelium. Instead it forms short thick segments which break apart from one another, and undergo a process of division and budding. These segments are termed hyphal bodies. The process is continued until the body cavity is almost wholly filled with them. Meanwhile, powerful enzymes are excreted which quickly dissolve the various internal structures of the host until practically nothing remains but the chitinous outer coat. Under unfavorable environmental conditions the hyphal bodies may assume heavier walls, and enter a period of rest as chlamydospores. On the return of favorable conditions they germinate quickly and proceed at once to the formation of conidiophores. In the more normal development chlamydospores are lacking and the conidiophores arise from the thin-walled hyphal bodies. They penetrate the outer covering of the host and form conidia in the air. In some species the primary hypha, without branching, abjoints terminally a single conidium. In others considerable branching may occur, each ultimate branch becoming a conidiophore. In either case the conidium is formed as a bud at the apex of the clavate termination of the conidiophore. It enlarges as the protoplasm of the conidiophore passes into it, and when the mature shape and size have been attained it is cut off from the

conidiophore by a transverse septum. This conidium is clearly the homologue of the sporangium of the Mucorales, and the

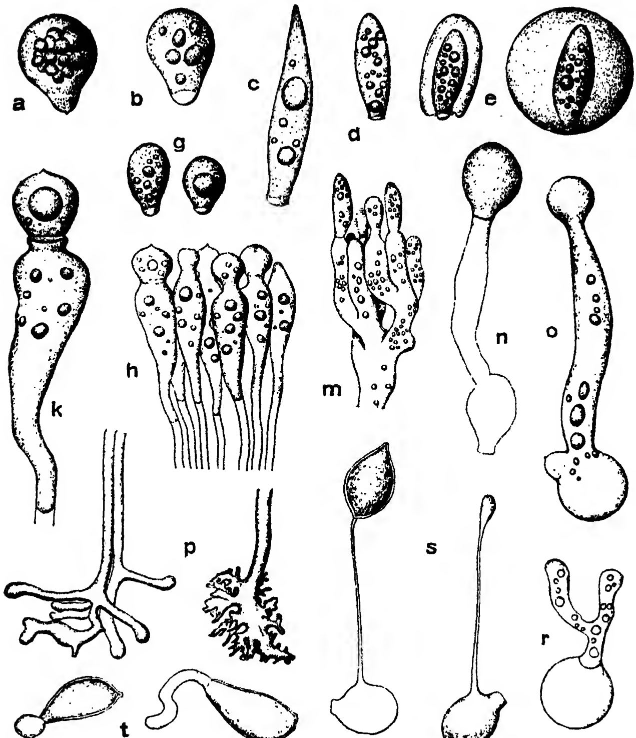

FIG. 107.—*Empusa spp.* (*a–d*) Primary conidia of four different species showing variation in shape. (*e, f*) Primary "conidium" after period in water showing spore floating free within sporangial wall; the conidium, therefore, a monosporic sporangium. (*g*) Primary conidium at left and secondary at right showing different form in same species. (*h*) Layer of unbranched conidiophores (*k*) One of these ready to discharge the conidium. (*m*) Branched conidiophores of another species. (*n, o*) Primary conidia germinating and forming secondary conidia. (*p*) Rhizoids of two different species, serving to attach host to substratum. (*r*) Germination of a hyphal body. (*s*) Primary conidia germinating by capillary tubes to form secondary conidia. (*t*) Germination of secondary conidia. (*After Thaxter 1888.*)

septum is essentially the same as the columella in that group. In fact as emphasized by Thaxter (1888: 143, *fig. 321*) the cell may

be regarded as a one-spored sporangium, for after it is cut off a second spore wall is formed about the protoplast. Although the two walls, that of the sporangium and that of the sporangiospore, are normally in close apposition they sometimes become so widely separated through the absorption of water that the spore may be seen floating in the sporangium (Fig. 107).

As the conidium approaches its mature size its contents and those of the conidiophore absorb water rapidly. The osmotic force exerted is greater in the conidiophore, and the septum is pushed into the conidium as a definite columella. Later the contents of the conidium becoming more dense, exert the greater pressure, and the columella is forced back into the conidiophore, its former position thus being reversed. Finally the pressure exerted is so strong that the outer of the two walls enclosing the conidium ruptures transversely in a circle about its base, and the conidium is discharged violently into the air and carried a considerable distance. The conidia of different species vary greatly in size, and range in shape from spherical to ellipsoidal. The wall is always smooth (never verrucose as in *Massospora*), and is covered with an adhesive material which serves to fasten the conidium to the object on which it falls. Should it fail to strike an insect host it may put out a germ tube, and, on this, form a secondary conidium which is in turn discharged. This process may be repeated until the vitality of the protoplasm is exhausted or a susceptible host encountered. Other more abnormal variations, in which secondary conidia bud directly from the primary or in which thicker-walled resting conidia are formed, occur under unfavorable conditions.

In most species the conidiophores emerge in great numbers from the host through the less resistant portions of its surface and form tufts or definite palisade layers evident to the unaided eye as felt-like masses, powdery with conidia. The color is usually white, but may vary to some shade of gray or green. Occasionally sterile hyphae protrude beyond the layer of conidiophores. These have been termed **paraphyses** by some authors and by others **cystidia.** As the host sickens and dies hyphae are sometimes pushed out from its body to anchor it firmly to the substratum. These are termed **rhizoids.** They occur chiefly in species having branched conidiophores.

True zygospores resulting from a sexual conjugation are formed in some species, but in others the resting spore is devel-

oped asexually (Fig. 108). The spore formed in the latter case is morphologically equivalent to the zygospore, and is termed the azygospore. The true zygospore is formed when two hyphal bodies or two mycelial cells conjugate. The young zygospore arises as an outgrowth from one of the conjugating cells, or may

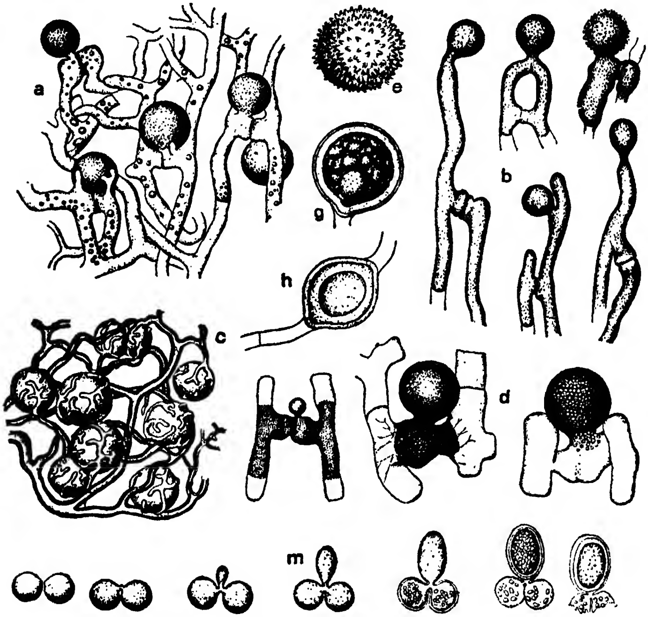

FIG. 108.—*Empusa spp.* (*a–c*) Zygospore formation between cells of hyphae in three different species. (*d*) Three stages in zygospore formation. (*e*) Echinulate zygospore typical of one species. (*g*, *h*) Terminal and intercalary azygospores. (*m*) Successive steps in conjugation of hyphal bodies to form zygospores. (*After Thaxter 1888.*)

bud out from their point of union as in *Piptocephalis.* At maturity it is usually large and spherical, and may be characteristically roughened. The fusing cells are plurinucleate. Though fusion of the nuclei in pairs at the time of zygospore germination was suspected by Riddle (1906: 184), it has not yet been demonstrated. In azygospore formation a bud is put out from a hyphal body or mycelial cell, and enlarges to form a spore similar to the

zygospore. The details of zygospore and azygospore formation are given by Riddle (1906) and Thaxter (1888).

The genus *Empusa* was founded by Cohn (1855) on the house fly parasite, *E. muscae*. The name *Empusa* had been applied earlier, however, to a genus of orchids, and Fresenius (1856: 882) recognizing this fact proposed *Entomophthora* to replace *Empusa* for the fungus genus. Later both names were used together in the Entomophthoraceae by Nowakowski (1884) and Brefeld (1877) for two distinct generic concepts. Nowakowski separated the known entomogenous species into three genera, *Empusa*, *Entomophthora*, and *Lamia*. His treatment was followed by others, including Schröter (1893) who uses it in Engler und Prantl's Die Natürliche Pflanzenfamilien. In this arrangement *Entomophthora* is characterized by branched conidiophores, the presence of rhizoids and cystidia, and the production, in at least some species, of true sexually formed zygospores. *Empusa*, as limited, lacks rhizoids and cystidia, has unbranched conidiophores, and forms azygospores instead of zygospores. *Lamia* is said to be intermediate, differing from *Empusa* chiefly in the possession of cystidia.

Thaxter (1888) who gave us the first really critical account of the group states that these characters are inconstant, and that border line species make the maintenance of this separation impossible. He unites all the species in a single genus under the name *Empusa*.

Some years after the appearance of Thaxter's paper Cavara (1899) studied cytologically two species, *Empusa muscae* and *Entomophthora delpiniana*, and found that while in the former the conidia are typically multinucleate, they are uninucleate in the latter. Riddle (1906) then investigated seven other species, and found that the conidia of the species which had been referred to *Empusa* are regularly multinucleate while those of the species placed in *Entomophthora* are uninucleate. Olive (1906: 202) obtained similar, though less definite, results in five additional species. He showed that the branching habit of the conidiophore is correlated with the uninucleate condition of the conidia. In forms such as *Empusa muscae* all the nuclei in the vegetative cell from which the conidiophore arises flow out into the conidium. In species like *Entomophthora sciarae*, on the other hand, the coenocytic conidiophore is divided by septa into uninucleate cells. Each cell then pushes out laterally and elongates until

the surface of the host is reached and penetrated. A branching conidiophore thus results, each branch of which abjoints terminally a single uninucleate conidium.

These observations indicate that the earlier usage of Nowakowski in applying the names *Empusa* and *Entomophthora* to species with unbranched and branched conidiophores respectively was probably in the main phylogenetically sound, and it is not unlikely that later students will return to it. However, the monograph of Thaxter has long been the standard treatment of the group, and the writer prefers to follow it in incorporating all the species in the single genus *Empusa*. Departure from this nomenclature at present would be premature, and result in changing various well known names. In any case additional species must be investigated cytologically before the nuclear condition of the conidium can be said to have unquestioned taxonomic value.

Thaxter's use of the generic name *Empusa* in preference to *Entomophthora* will be questioned by some students in the light of present rules of nomenclature. Although *Empusa* is the older, its earlier use in the orchids holds the possibility of confusion in the event of its future resurrection there. It has not seemed necessary in view of this somewhat unstable situation to use the family name Empusaceae or the ordinal name Empusales.

The genus *Empusa*, as here treated, is by far the largest genus of the family. Only four species were known to occur in the United States before Thaxter's monograph appeared. He described a total of twenty-six. At present approximately forty species are known.

The genus *Tarichium* Cohn (1875: 58) was based on the resting spore condition of an unknown species of *Empusa*. There is no reason, therefore, for recognizing it as a distinct genus.

The fungus described by Krassilstschik in 1886 as *Tarichium uvella*, and in 1888 redescribed by Sorokin as *Sorosporella agrotidis*, has been referred by various authors to the Entomophthoraceae. Recently it has been shown by Speare (1920: 399) to belong instead to the verticilliaceous hyphomycetes.

The green muscardine fungus, *Metarrhizium anisopliae* (Metsch.) Sorokin, which has been incorporated by some students in the Entomophthoraceae near *Empusa* is here excluded from the family. It apparently (Stevenson, 1918) belongs near *Penicillium*. It is an important parasite of many insects, some of

which are of considerable economic importance, and the literature dealing with it is very extensive. The following papers bear on the question of its taxonomic position: Friederichs (1920: 335), Speare (1912: *pl. 5, fig. a*), Rorer (1913: 88, *pl. 7*).

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CHAPTER XI

PHYCOMYCETOUS AFFINITIES OF THE HEMIASCOMYCETES

In the foregoing treatment of the Phycomycetes it has been emphasized (p. 21) that there are two well known opposing theories as to the origin of the fungi. One of these treats the group as an aggregation of relatively unrelated parts, which have degenerated along different lines from widely separated subdivisions of the algae. The other maintains that the fungi are monophyletic, and have arisen from non-chlorophyll bearing organisms lying below the level of the lowest of the present day Phycomycetes.

Advocates of the former theory regard the Phycomycetes and Ascomycetes as only remotely related, and believe the simplest of the Ascomycetes to be degenerate forms which have been derived in relatively recent times from more complex Ascomycetes. Adherents of the other theory maintain that the higher fungi have had a phycomycetous ancestry, and regard the simplest of the Ascomycetes as primitive and clearly related to certain of the higher Phycomycetes. In order that this latter point of view might be adequately presented for the consideration of the student interested in phylogeny it has been necessary to incorporate in the book the material composing this final chapter. This inclusion has been desirable from the standpoint of taxonomy also, since some of the forms treated by various authors as simple Ascomycetes are at best doubtful members of that group, and may be regarded by other writers as belonging to the Phycomycetes.

The essential features of the Ascomycetes have been enumerated above (p. 16) in the introductory chapter, and require little elaboration here. It should be recalled that the group is distinguished by the ascus, a sac-like cell forming endogenous spores called ascospores, usually in small and definite number (typically eight, less frequently some other multiple of two). It should be remembered too that the ascus and sporangium

are not homologous structures. The ascus is essentially sexual in character. In the young condition it is binucleate. The nuclei fuse, and the fusion nucleus, thus formed, undergoes three mitoses resulting in eight nuclei. At the close of the last mitosis the astral rays cut out the ascospores in the interior of the cytoplasm, the process being one of free-cell formation and thus differing wholly from that of progressive cytoplasmic cleavage by means of which sporangiospores are formed. In some Ascomycetes additional mitoses occur and the mature ascus is polysporic. The number of ascospores, even in such cases, may be definite, and is never wholly indefinite in the complete sense in which this is true of sporangiospores. The cytoplasm not incorporated in the ascospores is termed epiplasm, and functions in many species in maintaining turgor and in effecting spore discharge. Epiplasm is wholly lacking in the sporangium, though in a few forms a mucilaginous secretion lies between the spores and gives a similar aspect.

Though the ascus, strictly speaking, is not homologous with any structure in the Phycomycetes, and, in its typical form in the higher Ascomycetes, is clearly a new development, it gives evidence of having been derived from the sexual apparatus of the Phycomycetes rather than from the sporangium. The sporangium may be conceived to have given rise to the conidium in the Ascomycetes and Basidiomycetes as well as in the higher Phycomycetes. The Ascomycetes include a very large number of fungi, and in certain features of morphology are extremely various. In the standard classification presented by Schröter (1894) the group is split into the three primary subdivisions, Hemiascomycetes, Protoascomycetes and Euascomycetes.

The group Euascomycetes is much the largest of the three, and includes all the highly developed forms. In practically all of its members, asci are aggregated in definite fashion in a more or less conspicuous fruit body termed the **ascocarp.** In one of the major subdivisions of the Euascomycetes, known as the Discomycetes, the ascocarp is a typically open, cup-shaped or saucer-shaped body lined with a palisade layer of asci, and receives the special name **apothecium.** In another large group, the Pyrenomycetes, it is a typically closed, spherical or flask-shaped structure enclosing the asci, and is termed the **perithecium.**

The Protoascomycetes as treated by Schröter include the Saccharomycetaceae(yeasts), Endomycetaceae, Exoascaceae (leaf

curl fungi), and Ascocorticiaceae. These forms correspond with the Euascomycetes in that the ascus contains usually a small and definite number of spores, but they differ from them in that a definite ascocarp is lacking. The asci are scattered without order over a mould-like mycelium or exist as wholly isolated cells.

The Hemiascomycetes in Schröter's classification embrace a relatively small number of species, regarded by him as the most primitive of the known Ascomycetes. In the group, as characterized by him, a fruit body is lacking and the ascus contains a large and indefinite number of spores. He recognized for these forms three families, Ascoideaceae, Protomycetaceae, and Monascaceae. An additional family, Thelebolaceae, had meanwhile been erected by Brefeld (1891). These families in fact do not constitute natural groups, and subsequent investigation has shown that the genera included in them represent for the most part miscellaneous collections of unrelated, doubtful, or misunderstood fungi.

The family Thelebolaceae was founded by Brefeld (1891) on the single genus *Theleobolus* Tode (1790: 41), and was incorporated by him and by Lindau (1894; 1905) in the Hemiascomycetes. The genus name has been spelled by other authors *Thelebolus* and *Telebolus*. No other genus has been added to the family, and it is now recognized as closely related to *Rhyparobius* of the Ascobolaceae, a family of the Discomycetes. It is so treated by Saccardo (1928) and Rehm (1896). Two species, *Thel. stercoreus* Tode and *Thel. zukalii* Heimerl. have been studied cytologically by Ramlow (1906; 1914). Although the mature ascus is multinucleate and multispored it is enclosed in a definite fruit body and arises from a binucleate cell of a coiled archicarp such as occur in other genera of the Ascobolaceae. One to several asci are formed in the fruit body. The genus contains several species in addition to the two studied by Ramlow.

The family Monascaceae as presented by Schröter includes three genera, *Monascus* van Tieghem, *Helicosporangium* H. Karsten, and *Papulaspora* Preuss. Through the subsequent incorporation of all of these in other groups the family has automatically disappeared. In *Monascus* a definite ascocarp is formed resembling that of the Aspergillaceae, and the genus is clearly a member of that group. The early deliquescence of the ascus walls, and the consequent freeing of many spores into

the central cavity of the fruit body led van Tieghem to regard the latter as a multispored ascus. The papers of Barker (1903), Ikeno (1903), and Olive (1905) have clarified the situation. The position of the Aspergillaceae in the classification is discussed below. The genera *Helicosporangium* and *Papulaspora* have been studied in recent years by Hotson (1912). He merges them under the latter name, and regards the group as a form genus characterized by peculiar vegetative structures called **bulbils** which are evidently merely sclerotia of loose structure. The genus must be included in the group of sterile fungi with such genera as *Ozonium*, *Sclerotium*, and *Rhizoctonia*. Its species have been shown to have fruiting stages representative of various groups of the fungi. Complete misinterpretation of the nature of the bulbil led to the inclusion of these forms in the Hemiascomycetes.

The family Protomycetaceae, as treated by Schröter, includes two genera *Protomyces* Unger (1833) and *Endogone* Link (1809). These are not in fact closely related. *Endogone* has been discussed in a preceding chapter as a member of the Mucorales. As now understood the Protomycetaceae include three genera, *Protomyces*, *Protomycopsis*, and *Taphridium*. These constitute a coherent group of definitely related forms. The species are all parasitic in higher plants. The mycelium consists of delicate, intercellular, septate, branching hyphae, which bear large, globose to ellipsoidal, thick-walled, unicellular **chlamydospores** as terminal or intercalary enlargements. The chlamydospore after a period of rest germinates by the rupture of the thick exospore and the extrusion of the thin endospore as a globose or cylindrical sac. The contents of the chlamydospore, before or after passing into the sac, are broken up into a large number of small unicellular spores. These are disseminated by the violent apical rupture of the sac, and after their escape may undergo copulation in pairs. In germination they produce the endophytic mycelium directly, or in nutrient solutions bud like yeasts. The chlamydospore is multinucleate in young stages and is probably so from the first, the nuclei being scattered without order throughout the cytoplasm. In *Protomyces* and *Protomycopsis* they pass over thus with the cytoplasm into the sac-like extruded endospore (Fig. 109). Vacuoles then appear, and when the sac is fully formed the cytoplasm and nuclei constitute a thin peripheral layer surrounding a single large central vacuole.

This layer at maturity is split by cleavage planes to form many small, prismatic, uninucleate segments lining the wall. These may well be termed spore mother cells, for the nucleus in each divides twice to give four, and four uninucleate spores round up in each. Finally these spore tetrads break apart and the spores recede from the periphery of the sac to become aggregated in a ball near its tip. They are then ready for discharge. In *Taphridium* essentially the same condition exists, except that the spores are formed at the periphery of the chlamydospore before

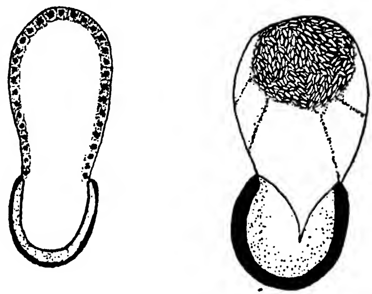

FIG. 109. (*a*) *Protomyces pachydermus* Thüm. Chlamydospore with extruded sac-like endospore in section at stage when spore-mother cells line the sac. (*b*) *P. kriegerianus* Büren. Later stage; the spores aggregated in the apical region of the extruded sac. (*After Büren 1915, 1922.*)

the extrusion of its endospore to form the sac. The two nuclear divisions concerned in the formation of the spore tetrads perhaps accomplish reduction but the point is as yet in doubt. It is not certain, moreover, that nuclear fusion occurs in the copulating spores.

The genus *Protomyces* Unger (1833) is the largest of the three composing the family. Büren (1915; 1922) gives a thorough taxonomic treatment of its species for Switzerland. The type species, *P. macrosporus* Unger, is confined to the Umbelliferae, but is composed of at least seven distinct biologic races. Ten or more species occur on Compositae. Cytological conditions in the genus have been studied chiefly in *P. macrosporus* and *P. pachydermus*. The cells of the mycelium are multinucleate. The papers of Büren (1913; 1914 *a*, *b*; 1915; 1922), Popta (1899),

and Juel (1902 *b;* 1921) constitute the literature on the cytology of the forms. Ramsbottom (1915; 1916) has contributed valuable comments on these. In *Protomyces* the endogenous spores are delimited within the endospore after its extrusion, the chlamydospores are intercalary with a smooth membrane, and the endogenous spores copulate regularly in pairs.

In the genus *Protomycopsis* Magnus (1905) the endogenous spores are formed within the extruded endospore as in *Protomyces*, but they do not copulate. The chlamydospore is, moreover, terminal and provided with a warty exospore. The genus includes at least eight or ten species (Büren, 1915; 1922), the type being *Protomycopsis leucanthemi* Magnus on *Chrysanthemum leucanthemum.*

In the genus *Taphridium* Lagerheim & Juel (Juel, 1902 *b*) the endogenous spores are delimited in a peripheral layer within the chlamydospore before the extrusion of its endospore. The genus, as known at present, embraces three species, *T. umbelliferarum* (Rostrup) Lag. & Juel on Umbelliferae, *T. rhaetica* (Volkart) Maire on *Crepis spp.*, and *T. algeriense* Juel on *Ferula communis.* The first named is the type of *Taphridium*, the second the type of *Volkartia* Maire (1907:145). Due to ignorance of life cycles and to varying conceptions of generic limits the nomenclatorial situation here has become much confused. In the light of present knowledge the merging of *Taphridium* and *Volkartia* seems necessary. In at least one species the spores have been described as fusing in pairs after their escape.

The position of the family Protomycetaceae in the natural system is in doubt, any disposition of it being to an extent dependent upon the interpretation given to the structures and phenomena just described. Unless the extruded endospore be regarded as a many-spored ascus there would seem to be no reason for incorporating these forms in the Ascomycetes. The earlier view of de Bary that these fungi are intermediate between the chytrids (Chytridiales) and smuts (Ustilaginales) is at least suggestive. Büren (1915), in his earlier work, regarded the spore mother cells as comparable to asci and termed the whole sac a synascus. He was inclined toward this point of view by his assumption that nuclear fusion occurs in the young chlamydospore. His later observations (Büren, 1922) led him to reverse his opinion, some evidence of nuclear fusion in the copulating

spores having been obtained. Juel (1921) attempts to homologize the chlamydospore in this group with the fertile cells of the ascogenous layer in the Exoascaceae. Gäumann (1926) and Gäumann and Dodge (1928), following this conception, embrace the two families in the single order Exoascales. To the author there seems to be no justification for this point of view, inasmuch as the spore sac of *Taphrina* and *Exoascus* is clearly an ascus of a high type. As treated here the Protomycetaceae are regarded as of unknown relationship. They may represent an isolated line of development with a phycomycetous ancestry, but there is no sure basis for their inclusion in the Ascomycetes. Until their nuclear history is better understood it would be futile to attempt to treat the group more definitely.

Of the families included by Schröter in the Hemiascomycetes the Ascoideaceae alone remain for consideration. Two genera *Dipodascus* Lagerheim (1892) and *Ascoidea* Brefeld (1891) were incorporated in the family by Schröter, two others, *Oscarbrefeldia* Holtermann (1898: 6) and *Conidiascus* Holtermann (1898: 23), were added by Lindau. There is insufficient evidence to show that any two of these four genera are in fact closely related.

The genus *Dipodascus* was based on a single species and is still monotypic. This species, *D. albidus* Lagerheim, was first discovered by its author in Ecuador growing in a slime flux from one of the Bromeliaceae. He obtained it in pure culture, and studied it in the living state. Nine years later it was found again by Juel (1902 *a*) in Sweden, where it occurred in a similar exudation from a wounded birch. Apparently only these two widely isolated collections have been made. Subcultures from Juel's material were widely distributed, and the fungus was studied in many institutions. The writer carried it in culture through many transfers over a period of years, but it has now died out, and is apparently no longer available in culture elsewhere. Probably it is not uncommon in nature, but if reisolated it should again be made widely available.

The fungus forms a white mat of profusely branching, septate hyphae, composed of multinucleate cells. At the tips of some branches oval, unicellular, multinucleate, hyaline oidia are formed. A definite sexual process occurs, numerous gametangia being formed over the mycelium. The gametangia arise in pairs as short lateral outgrowths from adjacent cells of the same hypha, or are cut off as terminal cells on different hyphae. In

either case they are multinucleate from the first and are morphologically indistinguishable. They come in contact near their tips and fuse, a wide opening resulting. The female cell (**ascogonium**) then pushes out at its apex, and elongates to form a long flexuous tube which tapers to a slender termination. The male cell (**antheridium**) does not increase in size, but retains its identity, so that the elongated ascogonium seems at maturity to have a forked base. The nuclei of the antheridium mingle with those of the ascogonium, and one of the male nuclei fuses with one of the female to form a single large fusion nucleus. This fusion is figured by both Juel (1902 *a*; 1921) and Dangeard (1907). Following fusion, repeated nuclear divison results finally in a large number of small nuclei. These are distinguished with difficulty from the supernumerary sexual nuclei. The latter tend to sink toward the bottom of the cell, while the progeny of the fusion nucleus retain their position in its upper end and become the centers of uninucleate spores. The spores are accompanied by intersporal substance, and are said by Juel to be cut out as in higher Ascomycetes by free cell formation. They are termed ascospores, and the elongated ascogonium which bears them is then called the ascus. It ruptures apically at maturity and the spores are extruded in a mass through a definite pore. They are globose to ellipsoidal, hyaline, and smooth.

The inclusion of *Dipodascus* in the Ascomycetes seems to be completely justified by Juel's observations on stained material. Though the ascogonium and ascus here are essentially the same structure, and though ascogenous hyphae and ascus hooks, common in higher Ascomycetes, are lacking, two features typical of the ascus of the Euascomycetes are present. There is a fusion of a single pair of sexual nuclei, and the spores are thought to be delimited by the astral rays. The multispored character of the ascus emphasized by Schröter is of little significance, since this condition exists in various higher forms also. In an interesting discussion of the phylogeny of the Ascomycetes Atkinson (1915) presents arguments supporting the hypothesis that that group arose from phycomycetous ancestors through forms such as *Dipodascus*. From this point of view *D. albidus* is the most primitive of all the known Ascomycetes, and may be regarded as perhaps showing relationship with species of the genus *Endogone* which is placed by various authors in the Mucorales (p. 265). The complete life cycle in the last named genus is

unfortunately not yet known. In the Ascomycetes genera such as *Eremascus*, *Endomyces*, and *Zygosaccharomyces* afford forms intermediate in type between *Dipodascus* and the Euascomycetes. In these genera also, the cell formed by the fusing gametangia functions as the ascus, but the ascospores are of small and definite number. In the multinucleate character of its gametangia *Dipodascus* stands alone among these lower forms. Its nearest known relative is perhaps *Endomyces magnusii* of the Endomycetaceae. In that species the ascus results from the fusion of uninucleate cells and only four ascospores are formed, but the cells of the mycelium and the oidia are multinucleate. In the other species of *Endomyces* all the cells are uninucleate. In some higher forms (*e.g.*, *Sphaerotheca*) the mature ascogonium is septate and one of its cells becomes the ascus.

Though *Dipodascus* is clearly ascomycetous, the three other genera, *Ascoidea*, *Conidiascus*, and *Oscarbrefeldia*, included with it in the Ascoideaceae by Schröter and Lindau, are of doubtful affinity.

In *Ascoidea* the mycelium is abundantly septate, repeatedly branched, and saprophytic, and a spore sac containing many spores as in *Dipodascus* is formed. The genus has been inadequately investigated, and accounts based on cytological studies are contradictory (Popta, 1899; Lohwag, 1926; Varitchak, 1928; Walker, 1929). Apparently a fusion of sexual nuclei does not occur, and the spores seem not to be delimited by the astral rays. The spore sac is ovate to clavate-cylindrical, is formed terminally, and dehisces by an apical pore. After the escape of the spores it proliferates repeatedly as does the sporangium in *Saprolegnia*. In the light of present knowledge there seems to be little justification for regarding this sac as an ascus. However, in a discussion of the origin of the Ascomycetes Atkinson (1915) takes the position that *Ascoidea* may be related to *Dipodascus*, and that the spore sac may be merely the result of the apogamous development of one gametangium in the absence of the other. Perhaps from that point of view the term ascus could be logically applied. Under certain conditions cells morphologically equivalent to the spore sacs function as conidia, falling off and germinating by germ tube. The first conidium formed is terminal on the hypha, but further apical growth of the hypha pushes it aside and causes it to have a lateral position. Successive formation of conidia in this fashion results in a

terminal cluster. The spore sac and the conidium are clearly one fundamental structure undergoing two types of germination. Even in proliferation a conidium may form within the old sac after the escape of the spores.

The genus was founded on a single species, *A. rubescens* Brefeld (1891) isolated from a slime flux of beech in Germany. A single other species, *A. saprolegnoides* Holtermann (1898) was described from Java where it was found forming a brownish encrusting mat on various trees. In the first species the spores

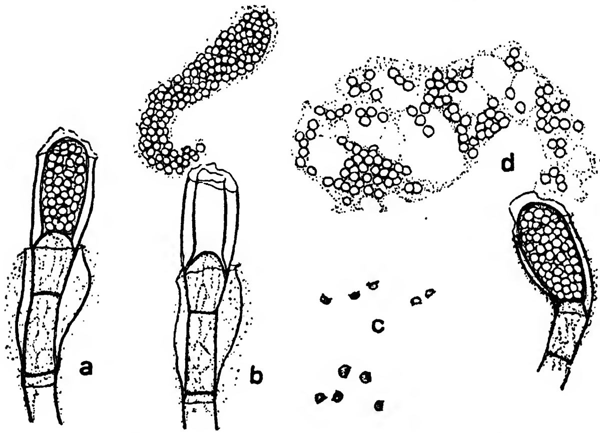

FIG. 110.—*Ascoidea rubescens* Brefeld. (*a*, *b*, *d*) Spore-sacs proliferating. Spores freed in an oily matrix. (*c*) Hat-shaped spores. *(From unpublished drawings by Leva B. Walker).*

are hat-shaped and lie in the sac with the flattened sides together. They are extruded in a long coiling thread-like mass. The second species as described differs chiefly in having globose to oval spores, not in pairs, which when extruded do not form a thread. In *A. rubescens* the empty walls of several spore sacs commonly are found nesting one within the other. In *A. saprolegnoides*, elongation of the thread is said to result usually in the formation of each successive sac beyond the limits of its predecessor. In spite of these described differences it is possible that the two species are the same. The hat-shape of the spore is not always observed with ease in *A. rubescens*, and may actually occur in Holtermann's species.

The genus *Oscarbrefeldia* is monotypic, having been based on *O. pellucida* Holtermann (1898), isolated in Java from a slime flux of trees. The mycelium is septate and bears ellipsoidal conidia similar to those of *Ascoidea.* Frequently also, cells indistinguishable from the conidia in shape and position form definite oval endogenous spores. Though Holtermann states that the spore number varies from one to seventy, his figures show it to be frequently eight. The spore sacs are sometimes formed in chains. Proliferation does not occur. As figured the spores are seen surrounded by epiplasm, but stained preparations were not made, and no evidence that nuclear fusion or free-cell formation occurs in these cells is provided. The author's figures and statements are confusing and unconvincing,

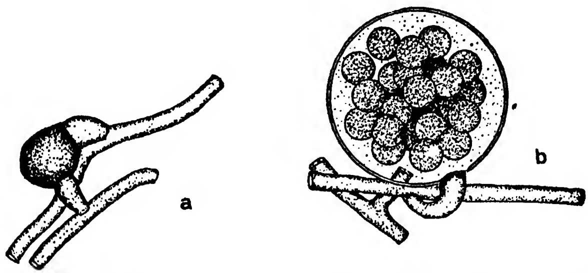

FIG. 111.—*Pericystis alvei* Betts. (*a*) Copulation of gametangia to form a sac. (*b*) Mature sac containing spores. (*After Claussen 1921*).

and we are left in doubt as to the real nature of the form studied. No adequate proof of its relationship with *Dipodascus* or *Ascoidea* is given. The genus is at best of doubtful position.

The genus *Conidiascus* is of similar status. It also is monotypic, having been based on *C. paradoxus* Holtermann (1898: 23), found in Java in a slimy exudation from *Ficus.* The mycelium forms a mat of septate, branching hyphae at whose tips oval conidia cluster as in *Ascoidea.* In cultures of distilled water the contents of a few conidia were observed to round up to form three to five globose spore-like bodies. In such cases the terms sporangium and ascus are used indiscriminately by Holtermann. He figures the escape of the spores through a simple pore at the end of the cell. No evidence of nuclear fusion or free-cell formation is given. Though the species may yet be shown to

be related to *Endomyces* its ascomycetous character is still in doubt.

In recent years another genus has been described which seems to fall near *Dipodascus*. It has been studied by Betts (1912) and Claussen (1921) and bears the name *Pericystis* Betts. It is based on a single species *P. alvei* Betts occurring in hives of bees, where it causes a well known trouble termed chalk brood. The fungus is heterothallic, and a multispored globose sac is formed by the copulation of a pair of gametangia much as in *Dipodascus*. The nuclear history is not known, but in general aspect the fungus seems to be intermediate in type between *Dipodascus*, *Endogone*, and *Eremascus* (Eidam, 1883). Its cytological study should prove very interesting.

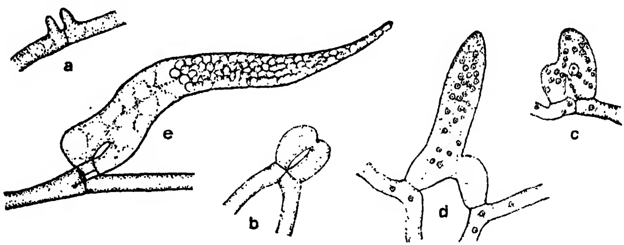

FIG. 112.—*Dipodascus albidus* Lagerheim. (*a*) Young progametangia. (*b*) Fusion of gametangia. (*c*) Female gametangium showing fusion nucleus. (*d*) Young ascus. (*e*) Mature ascus containing spores, (*b*, *after Lagerheim; c, after Juel; others from material.*)

All the members of the Hemiascomycetes, as that group was conceived by Schroter, have now been discussed. The ascomycetous character of several of these is much in doubt, but until further investigation is carried on none of them may be placed with complete assurance in the Phycomycetes. Only a few may be regarded as constituting connecting forms between the two groups. Of these *Dipodascus albidus* is the most unquestioned.

Recently Gäumann (1926) has presented a scheme of classification in which the Ascomycetes are split into the two major subdivisions Hemiascomycetes and Euascomycetes. In his grouping the Hemiascomycetes include two orders, the Endomycetales, embracing the Dipodascaceae, Endomycetaceae, and Saccharomycetaceae, and the Exoascales, incorporating the Protomycetaceae and the Exoascaceae. Immediately above

these in his scheme lie the Gymnoascaceae and other similar forms of the Euascomycetes.

In another recent classification, that of Gwynne-Vaughan (1922), the Ascomycetes are subdivided into Plectomycetes, Discomycetes, and Pyrenomycetes. The first named group includes the Plectascales, Erysiphales, and Exoascales. The Plectascales are in turn subdivided into Endomycetaceae (including *Dipodascus*), Saccharomycetaceae, Gymnoascaceae, and Aspergillaceae.

The general nature of those separations indicates clearly the trend of modern thought with respect to the interrelationships of the Ascomycetes. It should be remembered, however, that not all authorities regard the simple forms as primitive. Some read the evidence in reverse order, and derive the simple forms through degeneration from the more complex. The student interested in studying the possible relationships between the Phycomycetes and Ascomycetes must in any case focus his attention on these forms with apparently intermediate types of morphology.

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